EVOLUTION

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PREFACE

This book has long needed revision. In the decade and a half since the appearance of the first edition, knowledge of the factors contributing to evolution has made giant strides. It should also be remembered that that edition was the first attempt to give a general account of evolution resting on a genetic background. There had been, in the few years before its publication, research articles dealing with the operations of the genetic mechanism under specified environmental conditions, but no attempt to apply the genetic concepts to evolution in general. There was no precedent for a treatment of evolution as a whole from the viewpoint of genetics. The author had to feel his way in that pioneer presentation. One error of the original plan was limiting the account practically to the evolution of animals, which meant omission of one important source of change, namely, polyploidy.

Since the publication of the first edition there have been a number of excellent works on limited phases of the evolution problem, and one which treated the whole subject in a broadly genetic way. The latter book, however, was addressed to trained biologists. In contrast to it, this book is written for students—who may often lack some of the knowledge which moderately advanced undergraduate courses in biology would give them. The first edition was used in the author's classes, which included many students who had no previous biological training, and it is hoped that the revision may meet the same needs. Students without biological knowledge before their study of evolution have had to work harder than others, but they have demonstrated that they can attain rather satisfactory results. At the same time, there may be some professional biologists, interested chiefly in other phases of their subject, to whom the students' approach will appeal. Such biologists may easily skip the chapters in which they are already competent.

Many of the characteristics of the book are determined by its design for students. The early chapters giving the classical types of evidence for evolution are included because students are the presumed audience. It is not that present-day students need to be convinced that evolution has happened, for with rare exceptions they hold that view already. It is merely that they should know why they hold it. In this age too many

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people have opinions whose bases are not clear to them. These evidential chapters have been moderately changed. The treatment of geographic distribution has been expanded to include operations on a continental or world-wide scale, with examples of the resulting phenomena. The paleontological evidence has been recast to make more direct and emphatic the bearing on evolution theory of trees of evolution of such animals as the cephalopods, the horse, camel, and elephant. Where numbers of fossil species are involved, these have been changed to reflect the increase of paleontological knowledge. Numerous smaller changes have been introduced throughout these chapters.

The rest of the book has been completely rewritten. No attempt has been made to preserve any part of the old chapters which the new ones supplant. Only one-fifth of the illustrations are retained from the former edition, and two-thirds of the new illustrations are drawings made, or photographs obtained, expressly for this book. Many of the borrowed illustrations have never been used in connection with evolution discussions, though they are strictly pertinent.

In this rewritten part genetics is everywhere in the forefront. Some general biology, such as cell division, has had to be included for the sake of students not already familiar with the facts. The genetics, some of it fairly elementary, is split up and presented piecemeal in connection with the evolutionary phenomena to which it relates. Polyploidy, now it is hoped adequately discussed, is thus divided and treated at several points. Only a small degree of repetition is involved in this scattering of the genetic foundation, and the second and third references to a phenomenon are by implication commonly labeled as such. The author is convinced that comprehension of the genetic relations will by this method be much greater than if the genetic foundations had been collected into a separate chapter, far from their applications.

Related to the student clientele is the omission of citations of research articles and, mostly, names of contributors. Undergraduate students seldom refer to the original works, and consistent citation of such articles gives the text a choppy appearance. It has not been deemed necessary to refer always to the first published example of a phenomenon; and when a selection is made among several, it is possible that the best one has not always been chosen. The author shrank from the task of making close judgments in such matters when there was no expectation that his readers would gain appreciably. He asks the indulgence of investigators whose contributions might better have been used.

The history of the evolution idea in the first chapter should help in attaining an understanding of present attitudes on certain problems.

The author confesses to some doubt as to what were really evolution ideas in those early centuries, as distinguished from those that can merely be made to look evolutionary now.

Human interest has led to the expansion of the origin of man to form a separate chapter. It also helped to justify the chapter on organization of human and other animal societies. A more important reason for the discussion of societies was, however, to disabuse students' minds of a very common impression that biological evolution and societal evolution are one phenomenon—which, in man, they mostly are not. Man's egocentrism likewise led to a brief discussion of mutations caused by atomic energy and to some scattered animadversions on human mental processes, moral attitudes, and political proclivities.

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THE EVOLUTION CONCEPT OVER THE CENTURIES

> . . . the evolution idea is in itself the product of twenty-four centuries of evolution.
> —HENRY FAIRFIELD OSBORN, 1929

Evolution is a series of changes in which the nature of each step depends on what has gone before. Such related changes, produced by man or by natural forces, have occurred in many connections; accordingly there have been many evolutions. There has been an evolution of common law; the rules of human behavior, as they changed, leaned heavily on the code that existed previously. There has been an evolution of architecture, as designers of buildings seldom broke sharply with the past. The "beams" of English-style houses are merely symbolic of timbers that once had structural importance. Some of the apparently more radical changes have been largely importations from other areas where evolution of design took a different course. Men's clothing has undergone an evolution, with buttons being now preserved as ornaments at places where they used to be functional. Language, manners, morals, all have changed gradually, and never without reference to the past. The stars have been slowly modified; young, middle-aged, and old suns have their recognizable characteristics. Planets, including the earth, have developed step by step through the aeons. Chemical elements have been produced in a definite order, each new one having originated when the right conditions have come into being. Men's thoughts have never changed radically in a single step; they have always retained much of the flavor of their immediate antecedents. The sciences have changed, but new discoveries are never seen without relation to what was believed to be true just before they were made. The theory of evolution has had its dependent changes; the current theory, so different from that of less than a century ago, could not have arisen from that of Darwin's time without many of the steps which

have led up to it. Even the *process* of evolution, as should be obvious later, has had its evolution as the mechanisms through which it works have become modified.

The connected, interdependent series of changes that have occurred or are occurring in living beings is called organic evolution. Species, those elusive units of life in the mass, have been altered as new species arose from a few changed individuals of old ones, or even as all members of such a group were supplanted by a somewhat different type. In biological circles such change is what is meant by the single word "evolution," though biologists all recognize that the other evolutions have taken place. Every step of that evolution has depended on preceding steps. How the new has arisen out of the old is the subject matter of the greater part of this book. The reader may at points in this account detect steps that do not seem to be dependent on their predecessors, just as the turning up of the six-spot in dice is independent of other throws. Yet in a slightly larger field of relationships the usual dependence is there; no one turns up a six-spot unless one of the faces of the cubes bears that number of spots.

Early Evolutionary Thought. The units now called species, with which organic evolution is concerned, have doubtless been recognized by all peoples. Even primitive men knew that the animals and plants with which they were familiar were of different "kinds" and that there were many individuals of each sort. Some of these—game and edible plants—were of great importance to man and were recognized as the same sort of thing wherever they existed. The groups were not called species. Early peoples probably had no language symbol for the concept of groups of like individuals that differed from other groups.

Men also presumably observed that individuals of a kind were not all exactly alike. Whether they harbored any curiosity about the reason for such dissimilarities is a very different matter. Even today people take for granted the objects and relations that exist everywhere about them, never posing to themselves the questions of beginnings and causes that are inherent therein. Our only way to judge whether evolutionary ideas were held among peoples of the past is to find in their preserved writings the expression of conviction, or doubt, or antagonism, or inquiry. Since words, even apart from uncertainties of translation into another language, often mean different things to writer and reader, even written indications of evolutionary thought may be equivocal. These sources of misunderstanding explain the conflicting views of historians and are to be kept in mind by lay readers. A comment on human psychology may also be useful: those who seek

ardently to show that an idea was already old at any stipulated moment are likely to interpret doubtful passages as expressing that idea when others would consider the language irrelevant.

The most likely places to look for evolutionary ideas of early times are the treatises of philosophers, medical men, and naturalists. Records of medical practice are available as far back as the time of Homer in the ninth and eighth centuries B.C.; and the library of an Assyrian king of the seventh century B.C. contained treatises on medicine and botany. In none of these is there any reference to organic change. Yet slightly later two Greek contemporaries must be regarded as holding evolutionary views. These were Thales (640–546 B.C.) and Anaximander (611–547 B.C.). The writings of both these philosophers were lost, but references to them by others indicate their thought. Thales considered water to be the first principle; all things were derived from water. A marine origin of life is even now widely supported. Anaximander thought the earth was first fluid, and from its drying up all living things were produced. Men came first, but in the form of fishes. When these developed to a stage which could live on land, they burst their horny capsules and took on the human form. Man's helplessness after birth was regarded as evidence of his fishlike beginning.

The origin of life from nonliving matter, since called spontaneous generation or abiogenesis, included in both the above evolutionary sketches, was common to most philosophies of the early Greek period. Anaximenes and Xenophanes, both active in the sixth century B.C. and both apparently pupils of Anaximander, subscribed to this view. The former designated "terrestrial slime" as the material used and attributed to air the introduction of soul, life, motion, or thought into the physical body. Xenophanes also correctly regarded fossils as remnants or indications of former living things, and when these were of marine types accepted them as evidence of periodic submergence of the land. However, unless he considered the fossils to be genetically related to modern animals or to other fossils, that conclusion relates to evolution of the earth, not to organic evolution.

Enthusiastic searchers for early evolutionary theory would perhaps attribute such ideas to Heraclitus and Anaxagoras, both of the fifth century B.C. Heraclitus held, as one of three principles, that *everything flows*. That concept could apply to forms of life. It might be more difficult to see evolution in the postulate of Anaxagoras, that the universe was a chaos of innumerable seeds and that Mind brought order and form through a movement of rotation. Even skeptics, however, will see evolution in the processes which Empedocles (495–435 B.C.),

founder of the medical school in Sicily, imagined to occur. This poet, musician, and philosopher postulated abiogenesis, plants arising first, and animals successfully budding off from plants after many trials. All the changes resulted from the play of two forces, love and hate (or strife), upon the four elements, fire, air, water, and earth. Parts of animals arose separately and in unrelated order. When love predominated, the parts joined in random fashion. Most of the combinations were inviable, but the unions which were capable of existence formed the animals of the earth. One result, and perhaps purpose, of this theory was an explanation of the monsters of Greek mythology. The theory was a crude forerunner of the idea of survival of the fittest which has played so large a role since the middle of the nineteenth century. One passage in Empedocles is also interpreted as suggesting inheritance of acquired characters, in that the segmentation of the backbone in vertebrate animals is regarded as the result of repeated fractures produced by bending. It is of interest to point out that no guiding Intelligence or agent of Design is involved in the theory of Empedocles. Such outside or supernatural direction entered Greek philosophy in the same century, but from a different source and in different relations.

Aristotle. Appeal to an outside principle, a guiding Intelligence, was definitely part of Aristotle's philosophy. Both Plato and Aristotle considered Anaxagoras (see above) the first to introduce such an Intelligence. In the mind of Aristotle (Fig. 1) this agent became a perfecting principle; the guiding Intelligence worked toward an ever-improving living world. The result of the perfecting processes so directed was, in the living world, a succession of products, starting with lower plants, progressing to higher plants, through mollusks, arthropods, reptiles, birds, and (collaterally) fishes, mammals, and men. While such a chain could be the result of an evolution, each group resulting from a perfection of the one before it, Aristotle did not postulate that relationship. As Singer puts it, Aristotle was never quite an evolutionist, though he approached that position.

Yet according to Senn, Aristotle recorded all the common types of change—environmental modification, recombination as a consequence of hybridization, and changes that were presumably of the sort we now call mutation. Among the hybridizations he included some between genera, and these hybrids were regarded as fertile. Aristotle accepted inheritance of acquired characters which, much later, some evolutionists made the backbone of their theory of organic change. He was, however, unfortunate in his choice of the form of such in-

heritance. The form accepted by Aristotle was the inheritance of mutilations, which he held to be rather frequent. Inheritance of effects of use and disuse, however, he rejected. Had Aristotle reversed his selection, accepting use and disuse but rejecting mutilations, he might more readily have conceived a scheme of evolution. For adaptation was an important part of the scheme of the living world, and

FIG. 1. Aristotle, 384–322 B.C.

transmission of effects of functional activity could have replaced the outside Intelligence as the guide. In the view of modern geneticists he would have been wrong, even if he had concluded that effects of use are handed on; but he would have been recognized as an evolutionist.

When evolution was widely accepted, centuries later, chains of increasing complexity roughly like that of Aristotle's classification were pictured as stages in a single line of descent. Each group in such a chain was considered to have arisen by modification of the one before. It was not until the beginning of the nineteenth century that these chains were fully replaced by branching systems of classification. In

these it was recognized that each group might, and frequently did, give rise to several modified types instead of just one.

A pupil of Aristotle, Theophrastus, is said by Senn to have pointed out many changes arising in plants (the pomegranate, for example) by mutation, or spontaneous genetic modification. Wheat was regarded as being sometimes converted into rye grass. Both he and Aristotle are pictured as postulating considerable variability in species, but this would not necessarily be evolution.

Decline of Inquiry. Though the intellectual world owed much to Aristotle, this great philosopher and naturalist exerted one baleful influence. His guiding Intelligence was remembered more than his advocacy of the inductive method. That concept closes the door to inquiry. The outside agency leads to the concept of teleology, the purposefulness of events, which has ever been a bar to scientific progress. Cicero (106–43 B.C.) expressed the idea of teleology in the human body. Most philosophies included the idea of Design. Aristotle's works kept on being translated for many centuries, and by the sixth century the night of the Dark Ages was beginning to descend for other reasons than the appeal of mysticism (the repressive influence of religious leaders, for example).

In this long period there is little that resembles evolutionary thought. Pliny and Galen, representative of biology in the first and second centuries, did not touch upon the phenomenon of organic change. Julian the Apostate (331–363) discussed the action of soil and climate on men, which one historian accepts as evolution doctrine. Gregory of Nyssa (331–396) taught that creation was potential, that matter was endowed with the capacity to produce different things and over the ages exercised that power. The same idea was expressed more forcefully by the liberal churchman St. Augustine (354–430), who pointed out that the Scriptures were not a good source of scientific information. Though his stand was taken 1400 years before there was any theological call for such a statement, it implies a questionable sort of evolution concept.

The East. A modified form of the idea of potential creation reappears in the ninth century in the work of the Moslem theologian al-Nazzam. This writer held that Adam and his sons (descendants in general?) appeared in succession but were all created at the same time. Part of the creation was at once seen, the rest was hidden. The Moslem philosopher al-Jahiz, later in the ninth century, speculated upon the struggle for existence and the adaptation of living things to the environment. And al-Masudi, who died in Egypt in 957, in his

"Book of Indication and Revision," refers to some sort of relation or transition "from mineral to plant, from plant to animal, and from animal to man." Sarton calls this reference to change in the natural world a statement of views of evolution, but hardly of transformation of species into other species.

These last several items are part of the general intellectual dominance of the Arabs from the middle of the eighth to the end of the eleventh century; but Arabic peoples generally have not evinced much interest in theoretical biological matters.

In widely separated periods of time the idea of spontaneous generation has been expressed. The supposed origin of living things, of recognizable modern species, out of nonliving or dead matter, is merely a substitute for reproduction and is not evolution. Origin of living matter, not of any present species, perhaps scarcely recognizable as living, would be as much evolution as would the next step, production of a second species out of the first one. Sometimes it is not clear, in the writings of old philosophers, which view is being presented. Some such works belong in a history of evolutionary thought; others do not. Ibn Tufail discusses abiogenesis in a philosophical romance—a story of a sort of metaphysical Robinson Crusoe—written in the latter half of the twelfth century. This may have been general enough to be included.

Another Eastern work is that of Nizami-i-Arudi, written in Persian. It was a literary composition, full of anecdotes, and contained what some have regarded as evolutionary ideas. This writer pointed to concealed links, supposed connections between different groups of organisms, and curiously found them in corals, date palms, and monkeys. The first two were supposed to be links between plants and animals—date palms because they were recognized as having sex, which plants in general were not supposed to have. One may question whether such links were regarded as signs of genetic relationship; many comparisons have been made without implying kinship. Yet Sarton attributes evolution ideas to Nizami-i-Arudi.

Restriction by the Church. Over the centuries, ever since the time of Aristotle, the works of that Greek philosopher had been translated, interpreted, subjected to praise and some criticism, and used as a guide to the classification of knowledge. In the thirteenth century, to which our account has been brought, there were many new translations by both Christian and Jewish philosophers. This was ample evidence of the esteem in which he was held by presumably intelligent people. The church, however, was sensitive to some of the implications of

Aristotle's philosophy, or what was being taught as his philosophy. The Fourth Lateran Council in 1215 forbade the teaching of his work, except his logic and ethics. That proscription was gradually softened. By 1255 the Paris faculty permitted his entire teachings to be presented. Pope Urban IV (1261–1264) tried to restore the interdiction in part, but was only half-hearted in the attempt. Opposition was later apparently dropped entirely, then renewed. Aristotle's guiding Intelligence should have been acceptable to the church, but his philosophy as a whole had a rationalistic cast which seemed to make man a part of the general cosmic phenomena, like other animals, not something apart. It appeared to deny the immortality of man. It implied a contest between reason and faith—that was the interpretation put by the church on the teachings of Aristotle's followers.

The teaching of evolution has met the same opposition, and for the same reason. Some of its bitterest denunciations have come from the clergy. No one church has had a monopoly on the antagonism, though the denominations have differed greatly in the speed with which they have overcome their objections. Acceptance of the evolution theory has probably not been delayed by this conflict; it may even have been hastened, through a forcing of discussion where no consideration of the theory would otherwise have seemed in order. Little reference to the objections raised on doctrinal grounds will be made in the remainder of this review. The chief reason for mentioning them is to explain certain parts of the history of the idea.

Toward the Renaissance. With advancing time, more and more of the writings of philosophers and naturalists have been preserved, and the opportunities of assessing their thoughts are considerably increased. There is not, however, a comparable increase in evolutionary ideas. Men were simply not thinking about the transmutations of forms of life. Henry of Langenstein, one of the founders of the University of Vienna, who died in 1397, had astrological leanings and conceived that ever-new celestial combinations had caused new species of plants and animals to arise in the past and might be expected to produce new ones in the future. Even new types of men might take their origin from such changes in the complexity of nature. He believed in spontaneous generation, but of the kind that does not constitute evolution (mice from putrefying matter, for example).

Leonardo da Vinci (1452–1519) observed shells in the upper levels of the Apennines, knew they were of marine types, and concluded that they must once have been under the sea. But for Leonardo, just as for Xenophanes two thousand years earlier, this concept relates

only to evolution of the earth unless the shells were held to be related by descent to other kinds of shells or other animals.

That petals of flowers are modified leaves was suggested by Andrea Cesalpino (1519–1603) and more vigorously propounded by Goethe two centuries later. If the idea was that lines of descent gradually substituted petals for leaves, the change would be evolution. If identical entities were supposed to become petals in one part of a plant, leaves in another, or petals in some plants, leaves in others, the concept is one of individual development. Unfortunately the word "evolution" has been applied to the "unfolding" of the individual, as well as to change of race. The two meanings have no relation to one another, but writers, including some modern ones, have not always clearly distinguished between them.

The Natural Philosophers. The seventeenth and eighteenth centuries produced a group of thinkers who endeavored to find a common principle running through the universe and conceived life in terms of what it ought to be in this scheme of unity, not what common observation indicated that it is. More characteristic of Germany than other lands, the group is often called the *Naturphilosophen;* but it spread into other countries, particularly Sweden. No two reviewers, probably, would agree in detail as to its membership. Since it was characterized by its philosophy and general biological relations, and since we are looking only for early indications of evolutionary thought, it will be considerably dismembered in our account.

Francis Bacon (1561–1626) directed attention to variation and correctly called for a knowledge of its cause in arriving at an understanding of nature's course. Yet this variation would more readily introduce variety into old species than generate new ones. Whether with kinship in mind or not, Bacon points to intermediate forms, including flying fishes between fishes and birds, bats between birds and mammals, and mosses between putrescence and plants. As indications of kinship, these are not a great improvement over the connecting links of Nizami-i-Arudi.

The philosopher Descartes (1596–1650) was a proponent of evolution, but of the universe rather than of living things. Leibnitz (1646–1716) observed the variation of ammonites, fossil relatives of the pearly nautilus and the cuttlefish, and thought that the deep-sea conditions and other environmental factors had made species change. With respect to missing links, he held that none existed between man and the apes, unless on another world.

Immanuel Kant (1724–1804), famous philosopher on whom the

Naturphilosophen leaned heavily for their general concept of reality and mind, traced all higher forms of life back to simpler ones. He held that man had been changed by migration and changes of climate. He supported the idea of survival of the fittest as applied to groups (rather than to individuals) and thought mainly of races of men in this connection. Haeckel attributed these views to Kant as original with him, but most of them (including the survival of the fittest) had been expressed by Buffon, who antedated Kant by a couple of decades. Buffon, because his general ideas did not agree with those of the natural philosophers, is being reserved for the next section.

Several other romantic philosophers are put among the *Naturphilosophen* and *could* be put among the evolutionists *if:* (1) a scale of nature always means a line of descent (Lessing); (2) a law of perfectibility always works *through* imperfect stages to more perfect ones (Herder); and (3) diverse manifestations of a single force constitute related change (Schelling). These men did unquestionably influence others who specifically referred to the evolution process, and in this sense at least have a place in a history of the evolution idea.

No such doubt need be entertained about de Maillet (1656–1738) who, in a book named "Telliamed" (his own name in reverse), derived all terrestrial animals from marine ones by direct descent, birds from flying fishes, lions from sea lions (words often prove the undoing of people who use them), and man from the marine man who must have been the husband of the mermaid. All these changes were attributed to environment and habit. The author gives the details of the first of these changes, that of the flying fish which, caught by the wind or pursuing its chase too far, found itself on land and in its own lifetime became a bird.

Elementary particles were postulated by de Maupertuis (1698–1759), and these, possessing a certain order in parents, may be accidentally shifted into other orders in their descendants and produce the infinite variety of species. Modifications due to habits result in intersterility, keeping the species separate. The supposed shifting of order of elementary particles might seem to some almost prophetic of recombination of genes, now recognized as an important part of the evolution process; and in referring to intersterility de Maupertuis touches on one of the difficulties of modern evolution theory, but his proposed solution is not so happy or is at best a confusion of cause with effect.

Belonging to the thought of this time, though actually far out of chronological order, is Lorenz Oken (1779–1851). All life, to him, is

from the sea; the whole sea is alive. Love arose out of sea foam. Man was developed, not out of nothing, but of an earth clod or carbon, molded into form by use of water, and life, namely, air, was breathed into it, whereby galvanism or the vital process arose. Earth, water, air —one wonders what has become of fire, the fourth element of the early Greeks, that this nineteenth-century philosopher omits. Oken postulated that the skull of vertebrate animals consisted of fused vertebrae, but that would be an evolutionary concept only if their ancestors were supposed to have vertebrae in the head region. The comparison does not necessarily imply change with descent.

The poet Goethe (1749–1832) is unreservedly put among the evolutionists by Haeckel. Goethe was the first to declare his belief that man arose from other animals. His metamorphosis of plants (1790), involving conversion of leaves into flower parts, is usually considered such change. He entered into comparative anatomy which could be the base of evolution theory, and he supported the idea that the vertebrate skull consists of vertebrae;

FIG. 2. Carolus Linnaeus, 1707–1778.

but when, in such studies, Goethe concludes that the tail of mammals can be regarded as an indication of the endlessness of organic existence, one may fairly doubt (and many have doubted) that *any* scientific principle is involved in *any* of his work.

Others of the Eighteenth Century. The centuries which produced the *Naturphilosophen* (the German name should help prevent any confusion with the English Natural Philosophy, an early name for Physics) continued to yield other sorts of evolutionists. Whether Charles Bonnet (1720–1793) should be mentioned is doubtful, for his "evolution" was primarily that of the individual. One generation contains the germ of the next, this germ contains the germ of the next, and so on—reminiscent of the concealed or potential creation of St. Augustine and al-Nazzam. Double meanings of words plague science as much as other branches of intellectual activity. But Bonnet also discusses transitional forms, missing (or present) links, including the flying fishes as between fishes and birds. Between birds and mammals,

he adds (to the bat) another "flying" mammal, the flying squirrel, and a flightless bird, the ostrich; and between plants and animals he adds the sensitive plant. How much evidence of evolution Bonnet saw in these intermediates is doubtful.

Linnaeus (1707–1778), the great systematist, produced a branching scheme of classification, the first system that was not a scale of successive forms. While the branching system fits evolutionary origins better than does a linear scheme, Linnaeus (Fig. 2) never saw that relation. In the early editions of his "Systema Naturae" he adheres to fixity (unchangeableness) of species, in the words "there are no new species." His basis of classification was likeness, not kinship. He saw no need for a dependence of likeness on genetic relationship. Still, in late editions of his great book he points to the genus (of today) as the species that was created, implying the subsequent splitting up into the present species. This origin of species was facilitated by hybridization. In agreement with this change in his views, the 1766 edition of his monumental work (the first was in 1735) no longer contained the words "there are no new species." Linnaeus had come to accept a limited amount of evolution.

Of the same period was Buffon (1707–1788, Fig. 3) whose views are mostly recorded in the editions of his "Natural History of Animals." Among his evolutionary observations was the fact that deep fossils are less like present animals than the shallow ones are. In early editions of his book he regards the gaps between species as unbridgeable (species were fixed), but by 1761 he had concluded that transmutations of species are common. The cause of change he found in alterations of land and sea, differences of food, climate, etc. The action of the environment here is direct, not through some activity of the animal which environment stimulates. The changes must have been thought to be inherited, to produce the effects Buffon recorded, though he never specifically pointed this out. He postulated a remote common origin of ape and man, of horse and ass, then promptly entered a denial which attributed all these forms to creation. Such contradiction has been considered by historians either uncertainty in his own mind, or sycophancy, or irony. Races of men were thought to be differentiated by environment. Artificial selection was recognized as the source of breeds of domesticated animals, and the same result could be produced in nature by migration. He conceived a struggle for existence, and the survival of the fittest. Buffon's whole life showed something of the contradiction which may be found in single writings. Rather, his views fluctuated, from belief in fixity of species in his early

years, to extreme advocacy of environmental transmutation from 1761 to 1766, then to neither fixation nor mutability but assumption of many different forms by certain specific types.

Erasmus Darwin (1731–1802), in his "Zoonomia," considered nutrition the cause of similarity of a child to its mother and consistently held that the change that has occurred in domesticated animals was of environmental origin. Yet his stress was not on *direct* action of the environment; in this he departed from Buffon's main thesis. Organs which animals need are produced by the irritation of the parts which

FIG. 3. Comte de Buffon, 1707–1788.   FIG. 4. Erasmus Darwin, 1731–1802.

would (and later do) produce them (horns, spurs), and these characters are inherited. Darwin (Fig. 4) traced all life to a single filament (the word carries no necessary implication of shape) endowed with the capacity of being excited by a stimulus. Many responses to stimuli were held to be transmitted to posterity. Osborn considers that this is the first clear statement of the theory of inheritance of acquired characters and points out that, published in 1794, it antedates Lamarck's first statement of this principle by eight years.

Lamarck, His Allies and Opponents. So often has inheritance of acquired characters been postulated by naturalists and philosophers over practically all the centuries that have known biology at all, that the uninitiated may wonder why, when that phenomenon is mentioned, the mind flashes back unhesitatingly to Lamarck. The reason is the highly developed argument which this Frenchman prepared in sup-

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port of the thesis. Most great ideas are attributed not to the first person to entertain them but to the first to expound them fully.

Lamarck lived from 1744 to 1829. During the struggle of his youth he developed an interest in botany and was given a post in the natural-history museum in Paris. Later, as a result of the French Revolution and the consequent reorganizations, he and the mineralogist Geoffroy Saint-Hilaire were made professors of zoology. Lamarck (Fig. 5) was to have charge of the invertebrates, Geoffroy the verte-

Fig. 5. Chevalier de Lamarck, 1744–1829.

brates. The great variability of animals gradually forced Lamarck to abandon the doctrine of fixity of species, which he had held, and to conclude that species had changed. This conclusion was first published in 1802, then greatly expanded in his "Philosophie Zoologique" in 1809. It is to the latter work that students turn for a study of his theory.

The gist of that theory is that activity of animals develops the parts engaged, produces modifications in them, and these alterations are transmitted to the offspring. Plants, not having a nervous system and so not being able to respond to

stimuli, could be modified by environment directly; but not so the animals. Lack of use may cause degeneration, and this too is inherited. Many other naturalists who called themselves Lamarckians postulated, for animals as well as plants, changes produced directly by the environment, as by temperature, light, or nutrition. But to Lamarck the environment merely stimulated animals to activity, and this in turn produced the change. Need of a structure was supposed to help generate it, but only through activity which the need stimulated. Lamarck apparently never knew of Erasmus Darwin; his development of the environment idea was an independent one.

Lamarck's scheme of classification was at first a scale of successive forms. By 1809, however, and more clearly in 1815, it was becoming a branching system. He did not appear to regard this as bearing in any important way on his evolution theory, even though now it is recognized that any classification based on kinship must be branching. No

"perfecting tendency" was introduced by Lamarck; he held evolution to spring solely from influence of the surroundings.

Lamarck's theory was actively supported by his colleague Geoffroy Saint-Hilaire (Fig. 6), who, however, disagreed with Lamarck in particulars. To Geoffroy it was the direct action of the environment, not use and disuse, which produced change. Direct changes could be harmful, and animals so modified perished and were replaced by others (survival of the fittest). Geoffroy also thought that the change

FIG. 6. E. Geoffroy Saint-Hilaire.

FIG. 7. Baron Cuvier.

might be sudden and considerable, not always slow and slight—an idea to which he was led by congenital malformations of individuals. He did not think, as de Maillet did, that large changes could occur in the lifetime of adult animals; but because of the size of the postulated changes between generations he was not impressed with the need to find intermediates between different types.

Lamarck was not so fortunate in the reaction of another colleague to his theory. That colleague was Cuvier (Fig. 7). His theory was opposed and belittled by Cuvier who, by that time, was in a superior position in the French Academy. Cuvier reversed the order of change of his ideas, as compared with many others, and first considered species to be changeable, later to be fixed. He was a student of comparative anatomy and fossils and as such was in possession of knowledge which is now regarded as important evidence of evolution. But similarities of anatomy meant to him only the general schemes which

the Creator followed with variations. And the differences in fossils at
different levels he explained, in common with others, by repeated
catastrophes followed by immigration of other types from parts of the
earth not visited by the cataclysms. Followers of Cuvier assumed that
the catastrophes were followed by creation in a new mold; d'Orbigny
needed 27 new creations to explain what he observed. Cuvier, how-
ever, specifically denied new creation and postulated immigration.

The influence of Cuvier, his powers of debate, and his standing in
government and social circles enabled him to suppress Lamarck's new
idea. More than that, they delayed the acceptance of the theory of
evolution itself in France some forty years beyond the time when
that theory was adopted by the other great intellectual nations.

The Post-Lamarckian Period. Lamarck's influence extended little be-
yond 1820; a somewhat embittered and poverty-ridden old age, and
blindness which made him dependent on his daughters, stopped his
further contributions. No one stepped forward at once to carry the
evolution banner. Between Lamarck and the year 1858, when natural
selection made its debut, only one writer gave any sustained support
to the evolution idea, irrespective of the method by which it was
supposed to have been effected. That writer was Robert Chambers
(1802–1871), his work "Vestiges of Creation." Published anonymously
in 1844, this book ran through ten editions in nine years, and finally
in a twelfth edition in 1884, after the writer's death, Chambers was
credited with its authorship. The book started with the evolution of the
solar system. On the biological side it represented direct action by the
environment as the main source of change. There was a perfecting
principle, but environment deflected it. Spontaneous generation of
simple animals was regarded as going on continuously, as a group of
electrochemical processes.

There were not wanting naturalists who sporadically gave expres-
sion to evolutionary views—enough of them that even to mention them
would magnify the merits of some beyond their deserts. Some of them
followed Buffon rather than Lamarck, in that they held environment
to act directly in producing change. Among these was the philosopher
Herbert Spencer (1820–1903), who wrote both before and long after
1858. Some adhered to a perfecting principle. Some of them adum-
brated, or even gave full expression to, the principle of selection, to
be developed so fully later by Charles Darwin. One of these selec-
tionists was Dr. W. C. Wells, in 1813, applying the principle to the
origin of black races in Africa; another was Patrick Matthew in 1831.
The latter was so impressed, much later, by his priority over Darwin

that he called attention to his authorship of the doctrine on the title page of other publications. Naudin (1852) also postulated selection, but it was hardly natural selection; it was the "needs" and "wishes" of Nature, not fitness, which made a choice among differing characteristics.

The existence of several selectionists before Charles Darwin does not mean that Lamarck and Buffon had been abandoned. Supporters of both these naturalists have continued to arise. There have been many adherents of the doctrine of inheritance of acquired characters, prominent among them American paleontologists. Naturalists and medical men have furnished their quota of supporters. Herbert Spencer has been mentioned; his "physiological units" were calculated to be the means of such transmission. Probably there are still advocates of the Lamarckian doctrine in important positions in biology. It must be said, however, that the group of biologists who should know most about heredity—the geneticists—are practically unanimous in their rejection of inheritance of acquired characters. They reject it not merely as a factor in evolution; they hold it does not occur.

FIG. 8. Karl Ernst von Baer.

Incidental support of the general idea of evolution was furnished by the embryologists, some of whom saw in the successive stages of the embryo indications of successively more complex animals of other types. Meckel (1811) saw the adult of low animals in the embryos of higher ones. Von Baer changed the comparison to point out that embryos of high and low types are more similar than are their adult stages. Von Baer (Fig. 8) in 1834 expressed forcibly the idea that species change, but he did not argue to that end from the similarities of embryos. That was reserved for Ernst Haeckel to point out, much later and much more fully than had Meckel, as the substance of his "biogenetic law." Von Baer was in general antievolutionist; his observations on embryos suggested evolution to others, not to himself.

Charles Darwin. Evolution ideas had arisen in the minds of so many that the coordinating effect of a rational fundamental theory could

probably not have been much longer delayed. It was Charles Darwin's fortune to live at the critical time. It was also to his parents' credit that he was endowed with the keen mind, the persistence, and the curiosity that were needed to carry him over the long, uncharted course of discovery and speculation. It was an accident that his health would not permit him to follow a regular occupation, and a great good fortune that he had means which made an occupation unnecessary. His flair for natural history, like tastes in general, will never be explained; it was exceedingly important in Darwin's life. Without

FIG. 9. Charles Darwin.

that penchant, expressed in his youth, he would never have been appointed to the naturalist's post on the voyage of the *Beagle*. Given Darwin's qualities, that voyage made him what he became. This expedition lasted five years (1831–1836), went around the world, and made long stops which enabled Darwin to make observations and collections on land. South America and the Galápagos Islands received considerable emphasis.

When he started this voyage, Darwin believed that species are fixed. Observations made on the voyage created misgivings in his mind. The change in the nature of fossils from north to south in South America; the peculiarities of island faunas, but their similarities to continental life; the great variability of animal groups; the similarities of fossils to modern animals—these things appeared to have no meaning in a world of unchanging species. Darwin began to suspect that species had been modified.
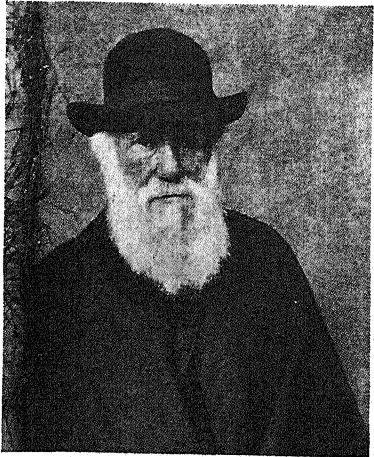
After the return of the *Beagle* in 1836, he began keeping a record of all the facts which seemed to him to bear on the question of such change. Within two years there came to him the idea which brought most of his recorded phenomena into a sort of harmony. In 1838 Darwin (Fig. 9) read an already old book by Malthus, entitled "Essay on Population," in which the author calls attention to the tendency to geometric increase in human populations and to the factors which would hold these populations in check. Darwin applied this concept to animals and plants. Many more individuals were being produced

than could survive, and many would perish. Which ones would be lost, which remain? Darwin conceived that this selection would be made by the qualities of the individuals. No two were alike, and any favorable qualities would enable their possessors to survive; less fortunately endowed individuals would perish. His explanation involved a struggle for existence with its inevitable winners and losers. This process has commonly been called natural selection. A general consequence of long-continued natural selection would be to create adaptation of living things to their environment, and such adaptation is ob-
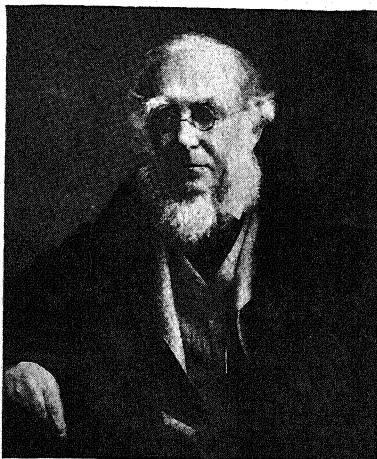
FIG. 10. Sir Joseph Hooker.

FIG. 11. Charles Lyell.

servable on every hand. This theory was in no respect like that of his grandfather Erasmus Darwin; but in later enlargements of the general concept of evolution Charles Darwin returned in part to the theories of Erasmus Darwin, Lamarck, and Buffon.

Darwin was in no haste to publish this theory, but kept on assembling facts which bore on it. He was in communication at intervals with the botanists Joseph Hooker (Fig. 10) and the American Asa Gray, and the geologist Charles Lyell (Fig. 11), beginning at least as early as 1844. Publication would doubtless have been much longer delayed but for the coincidence that another naturalist eventually conceived the same theory in a brilliant flash of mind. That naturalist was Alfred Russel Wallace (Fig. 12) who in 1855 had already written in vigorous support of the evolution idea. Then, in 1858, while Wallace was in the Orient observing the peculiarities of geographic distribu-

tion of animals, the idea of natural selection suddenly came to him. He too had read the book by Malthus and attributed to it his concept of survival of the favored. He sent a brief statement of the theory to Darwin to ask his opinion of it. Darwin would modestly have permitted Wallace to publish the result of a sudden inspiration and have withheld his own 20-year-old theory, but Hooker and Lyell objected. These two men arranged to have communications from both Darwin and Wallace read at a meeting of the Linnaean Society on July 1, 1858. The theory of natural selection was thus launched with dual

FIG. 12. Alfred Russel Wallace, just before his journey to the Far East.
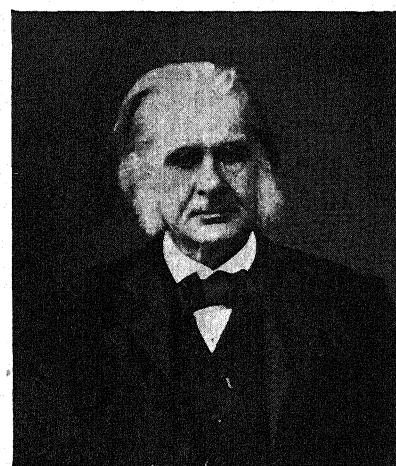
FIG. 13. Thomas Henry Huxley.

sponsorship. The scientific world has given most of the credit for it to Darwin; but the fact that two workers could independently arrive at the same conclusion indicates that the concept could not have been long postponed. It is in general true that, when the time is ripe for a great advance in science, if one person does not take that step another soon does.

Darwin expanded the idea of natural selection and the supporting evidence in his book "Origin of Species" in 1859. This book went through a number of editions, each one showing some modifications of the idea in detail, but not changing the fundamental concept. Certain special phases of the evolution problem were discussed in other books.

Champions and Opponents of Evolution. Darwin's old confidants were of course among his supporters, but Lyell was past his prime —anyway, he was a geologist, not a biologist—and Hooker was not militant. The lead in presenting Darwin's ideas to the general intelligent public was taken by T. H. Huxley (Fig. 13). In popular lectures and magazine articles and in formal debate with the churchman Wilberforce, Huxley bore the brunt of the campaign of education. Haeckel, in Germany, aligned himself strongly on Darwin's side, as did Gegenbaur from the point of view of comparative anatomy, and later Weismann in relation to the mechanism of heredity. The German botanist Nägeli also favored evolution, as did Fritz Müller. But von Kölliker was against, as was also von Baer in general, despite his recognition, already mentioned, that species were changeable. Oskar Hertwig was opposed. The Swiss-American Louis Agassiz never accepted evolution. In England, the anatomist Richard Owen ranged himself against Darwin and declared we are in complete ignorance of the way in which species arose. Owen weakened his position by writing in thinly veiled anonymity, referring to himself in the third person as "Professor Owen," the person on whom he relied as authority for his opposition to Darwin. The French did not figure in any important way in the argument over Darwin's theories.

Confusion of Evolution and Natural Selection. It is interesting to note, in the controversy just described, how much of it related to evolution, how little to natural selection. From the point of view of the present time, and in view of the many times the evolution idea had been expressed before Darwin, one might suppose that the argument would have concerned principally natural selection. The two ideas were, however, greatly confused. Darwin himself was guilty of this indiscrimination. In long passages his arguments relate to the idea that species have changed; but at the close of them he concludes that they indicate natural selection. Huxley's popular articles and lectures were, quite understandably, devoted mostly to evolution. The words "natural selection" crept into them, but it was change of species that he chiefly sought to establish. Haeckel (Fig. 14) was an enthusiastic supporter of Darwin, but he had little to say about selection. He was interested in the course of evolution, not in the factors which directed that course. Some of Haeckel's work could even be classed with the old *Naturphilosophie* and would have done credit to the Goethe-Schelling-Hegel romanticism. Darwin's supporters among the comparative anatomists were championing evolution (kinship of

present unlike types), not selection. Nägeli was an evolutionist, but postulated an inner force plus the Lamarckian effect. Weismann, on the contrary, was concerned primarily with selection, a distinction necessitated by his passion for the continuity of the genetic material.

The confusion of evolution with natural selection was great enough in Germany to lead to the use of the word *Darwinismus* to mean evolution. German is the only language in which the word coined from Darwin's name has that meaning. In other intellectual countries Darwinism has nearly always referred to Darwin's contribution to evolution theory, sometimes limited to his natural selection, sometimes expanded to include his Lamarckism and the pangenesis devised to explain it. In French the word for evolution is *transformisme*.

FIG. 14. Ernst Haeckel.

Later Development of Evolution Theory. A number of special forms of selection were proposed in the several decades following the publication of the "Origin of Species." They were designed to apply to certain types of supposed advantages and to explain certain specialized kinds of change of species. Then, toward the end of the nineteenth century, the validity of the natural-selection theory or the scope of its application began to come into question. A reaction against the theory continued over the turn of the century. But in the second, or certainly by the third, decade of the present century natural selection staged a vigorous recovery. At present, among geneticists, there is practical unanimity of opinion that selection furnishes the chief, but not the only, guide to the evolution process.

These later developments of evolution theory are so closely identified with the mechanisms by which the change of species is now held to be effected, that to discuss the history would involve discussing the mechanisms. Much repetition would be required, and it is unlikely that the connection could at this stage be made sufficiently clear to serve any purpose. These more recent features will accordingly be taken up piecemeal in close relation to the mechanisms and processes which lie at their foundations.
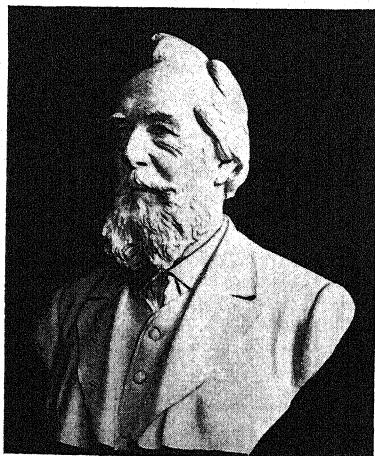
CHAPTER II

ORDER IN DIVERSITY AMONG
LIVING THINGS

> That it is possible to arrange all the varied forms of animals
> into groups, having this sort of singular subordination one to the
> other, is a very remarkable circumstance.
> —T. H. HUXLEY, 1863

The philosophers and naturalists who in the past two thousand years
and more have believed that kinds of animals and plants have changed,
that new kinds have sprung out of old ones, were not recording a
process they could observe. Even now the formation of new species
from some individuals of old ones can be witnessed only rarely and
in special sets of circumstances. The conclusion that evolution has been
happening is an inference from present-day ascertainable facts. It
is a verdict reached from circumstantial evidence, but circumstances
are often better evidence than is direct testimony. How valid the belief
in evolution is depends on how many things need it as an explana-
tion. If many observed situations are reasonably explained on the
assumption that species have changed, that new species have arisen,
and if these things have no other reasonable explanation, the theory
of such change has a fairly sound basis.

What are the observed facts which evolution of species explains, but
for which other imaginable causes are inadequate? In general this
circumstantial evidence falls into four classes. These are the subject
matter of the next four chapters. The fifth type of evidence, observa-
tion of changes which *could* lead to new species but which in most
instances have not been directly proved to do so, is scattered through
many of the subsequent chapters. That one of the four groups of cir-
cumstantial evidence which is most abundant, and closest at hand for
those who are able to use it, is the natural scheme of classification
which naturalists have been forced to adopt.

The living things on the earth present an almost inexhaustible array
of differences. Professional naturalists give testimony to the variety

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of life by becoming what are called ornithologists, mammalogists, conchologists, and the like, thereby confessing their inability to master more than a small section of the living world about them. How great this diversity is can be expressed numerically, but to do so it is necessary to decide upon the degree of analysis to which populations shall be subjected. If every detectable difference be recognized, it is probably true that no two organisms are alike; with such a standard the number of different kinds of beings is the number of individuals, which is almost inexpressibly large. If minor differences are to be ignored, then individuals must be grouped, and the number of groups depends on how large are the neglected distinctions. This is what taxonomists do in classifying both plants and animals—the greater the differences which they pass over, the fewer the resulting groups. In general classifications have sought to recognize all significant heterogeneity up to the point at which the number of groups becomes unwieldy. Taxonomists have disagreed concerning what is significant, and have differed in their opinions of what constitutes a too cumbersome system. At the present time, among animals, about 800,000 kinds have been described; and it is probable that, with the same standards but with all existent kinds discovered, the number would be far over a million. Indeed, certain types of reasoning have led to a figure twice as large. Among plants about 250,000 kinds have been described, and the total including those still unknown is estimated to be perhaps one-fourth larger. This is one of the more conservative estimates.

Degrees of Likeness and Difference. Naturalists at first supposed that these kinds of organisms, to which they gave the name species, had always existed as distinct from one another as they are now, and in the same form as at present. They were no more curious about the origins of species than they were about the beginnings of the universe; everything was supposed to have been created—a belief that left little room for, and certainly did not demand, any inquiry. In any case, the origin of one species did not need to be in any way related to the origins of other species. There are, however, within the classifications themselves, indications that such independence did not exist. When species are compared with one another, it is found that they display very unequal likenesses and differences. It is not possible to arrange them in a series from one extreme to another with evenly graded steps between the species. Even when a very limited portion of the animal or plant kingdom is employed for this purpose, such arrangement with uniform steps is still impossible. This is not due merely to the fact that species differ in several or many characters, and that

an evenly graded series based on one character cannot be dovetailed
into a series based on some other character. It is due rather to the fact
that some species resemble each other much more closely than they
resemble any other species. Half a dozen or more species of animal
differ from each other in relatively small ways; but when the rest of the
animal kingdom is searched for others as nearly like them, none is
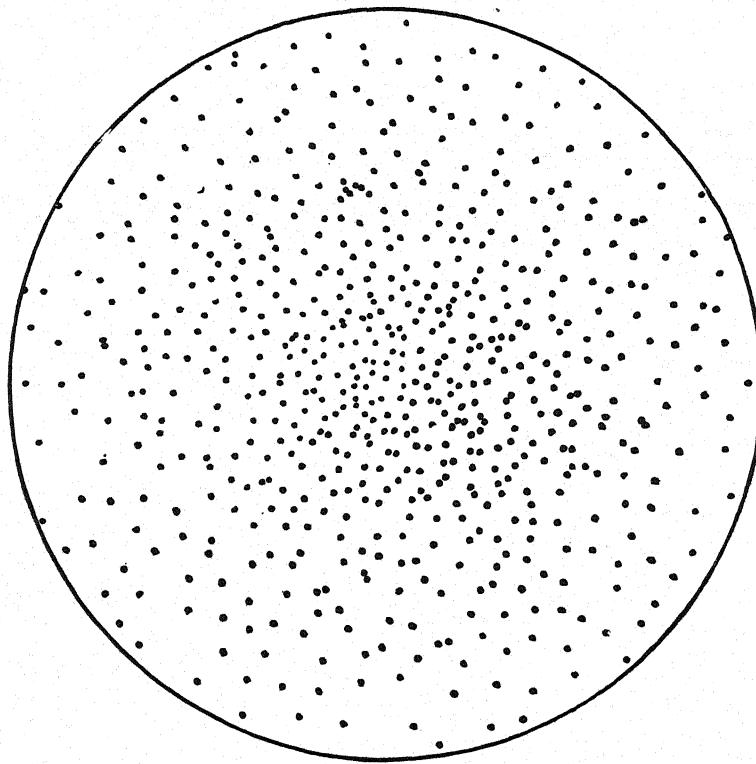
FIG. 15. Distribution of shot on a target. (*Remington Arms Co.*)

found. The most similar other species is separated from them by a
more distinct gap. This most similar other species may be one of an-
other half dozen or more which exhibit among themselves as great a
degree of similarity as did the first half dozen, but this group is sepa-
rated from the first by a greater difference than that between any two
species within either of the groups. All through the animal and plant
kingdoms species are capable of being thus grouped. The number of
species in any such group varies greatly; occasionally a species has to

be set aside by itself, but often there are scores of them in a group. This clustering of species is not merely something which the taxonomist may do if he chooses; it is something he must do if his arrangement follows the observed properties of the species.

Now, the different degrees of similarity and difference among species which make their collection into groups the obvious way of arranging them are hardly consonant with the view that the various species are and always have been independent of one another. If species were from the beginning independent, there would be no obvious reason for the existence of groups based on similarity. When the first few drops of a shower fall upon a dry pavement, they are not disposed in clusters according to any scheme. The shot from a shell when fired at a target (Fig. 15) are not systematically collected into groups separated by spaces of regularly variable widths. It would be difficult to find groups of half a dozen or a score of shot, or of raindrops, regularly separated from adjoining similar groups by spaces wider than those between members of the same group. If the shot on a target were distributed in such groups, with wider spaces between clusters than within them (Fig. 16), it would be inferred either that a number of the lead pellets had clung together for some time after leaving the cartridge but had separated before reaching the target, or that the balls had broken into fragments at some point between gun and target. In like manner, when species are found to be everywhere capable of being bunched on the ground of similarity, it is difficult to avoid the conclusion that they were, in their origin, in some way associated with one another.

Genera and Higher Groups. The species that resemble one another closely constitute, in the language of the taxonomist, a genus. It may be useful to illustrate the grouping described above by examples chosen from animals so well known that anatomical bases for the classification will not be required. These examples are taken from the birds of North America. There are some nine species of gulls belonging to the genus Larus. Likewise, there are in the same region nine species of terns assigned to the genus Sterna. Gulls are not very different from terns, but the difference between them is greater than that between two of the gulls mentioned, or between two of the terns. There are eight species of ducks, one of them the mallard, belonging to the genus Anas, and five geese belonging to the genus Branta. The difference between any one of these ducks and any one of the geese is greater than that between any two of the ducks or between any two of the geese.

The grouping of living things does not stop with the species. The genera are likewise subject to such arrangement. The gulls and terns, including half a dozen genera besides Larus and Sterna, are much more nearly alike than they are like any other birds. The ducks, geese, and swans, including a dozen and a half genera besides Anas and
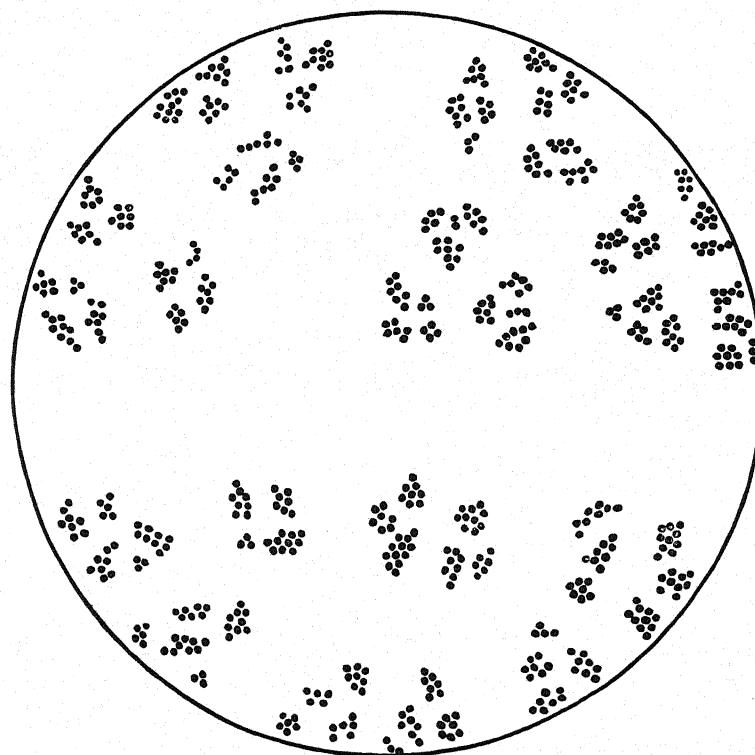
FIG. 16. A hypothetical grouping of shot on a target which would indicate some connection between the separate pellets—comparable to the grouping of species in genera, families, orders, and classes.

Branta, are more alike among themselves than they are like any others. In classification, these closer similarities are recognized by placing the similar genera into a family. The gulls and terns make the family Laridae, while the ducks, geese, and swans compose the family Anatidae.

In a similar way families are collected into orders. The gulls and terns (family Laridae), together with two other families (the skim-

mers, and the skuas and jaegers), constitute one order. The family of
ducks, geese, and swans constitutes an order by itself, since there is
no other family nearly enough like it to be included with it. Other
orders of birds are the herons, storks, and ibises; the sandpipers,
phalaropes, and plovers; the grouse, bobwhites, and pheasants; the
hawks, eagles, owls, and vultures; the woodpeckers; the whippoor-
wills, nighthawks, swifts, and hummingbirds; and the perching birds,
such as sparrows, tanagers, swallows, vireos, warblers, wrens, and
thrushes. To any one familiar with these birds, it is obvious that
those included in one order have more in common than any of them
have in common with birds of another order.

In the animal kingdom as a whole orders are collected into groups
of higher rank known as classes. All the birds belong to one class.
Contrasted with them, but more nearly like them than are any other
animals, are four other commonly known classes, namely, the fishes,
amphibia, reptiles, and mammals. Any bird is more like any other
bird than it is like any fish or reptile. Any fish is more like any other
fish than it is like any amphibian or mammal.

And yet all these groups (fishes, amphibia, reptiles, birds, mam-
mals) have important things in common, in which they differ from all
other animals. Chief among these is the bony skeleton which, in every
one of them, includes a segmented axis, the backbone. Another feature
is the position of the nervous system above or behind the digestive
tract, a position which it occupies in no other group of animals. This
greater similarity among these so-called higher animals than between
them and any others is recognized in classification by placing them,
together with several groups of less commonly known animals, in the
phylum Chordata.

There are a dozen other principal phyla. Without their technical
names, the chief of these phyla may be indicated as follows: the
insects, lobsters, centipedes, spiders; the clams, oysters, snails, cuttle-
fishes; the segmented worms and leeches; the starfishes, sea urchins,
sea cucumbers; the roundworms; the flatworms; the hydroids, corals,
anemones, jellyfishes; the sponges; and the unicellular organisms or
protozoa. While zoologists have attempted at times to discover signifi-
cant similarities between two phyla, as between insects, centipedes,
etc., on the one hand, and the segmented worms on the other, largely
because of the segmentation of the bodies in both, or have set one
phylum apart as distinct from the rest because of one or two striking
features, attempts to arrange all the phyla into a small number of
comparable groups of still higher rank have been of doubtful validity.

That is, the phylum is the most inclusive group all members of which possess undoubtedly significant similarities.[1]

Each phylum is constituted in essentially the same way as is the group Chordata. The Arthropoda, for example, fall naturally into four groups, the crustacea (lobsters, etc.), the centipedes and millipedes, the insects, and the spiders and similar animals.[2] Each of these groups, which are called classes, is naturally divisible into smaller groups, the orders. Thus the insects include 19 (more or fewer, according to different taxonomists) orders, of which the following will serve as illustrations: the bees, ants, and wasps; the butterflies and moths; the beetles; the flies; the grasshoppers and crickets; the termites; the dragonflies; and the May flies. Each order is divisible into families, naturally distinguished from one another, each family into genera, and each genus into species. In other words, the whole animal kingdom is classifiable according to the same general scheme. Plants are classified in a strictly comparable way, the only difference being that botanists have usually applied different names to the groups of high rank.

The Branching Arrangement. The important feature of the classification is that, according to it, the living world is composed of groups within groups. Regardless of the rank of a group, whether low (species) or high (class), it has certain resemblances which place it nearer to certain other groups of its own rank than to others. Everywhere the genera within one family are more alike than are any of the genera of different families; the families comprising an order are more alike than are any families of different orders; the orders belonging to one class resemble one another more closely than do any two orders of different classes; and so on.

As was pointed out in connection with species, this grouping within groups would not be expected if each group had arisen independently of other groups of the same rank. The several genera of a family must have been in some way interdependent in order that their present-day closer similarities might exist. Those orders which are especially similar, and are marked off from all other orders by greater differences,

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[1] This statement ignores the fact that, regarding several phyla as proposed by various taxonomists, but not regarding any of the principal ones mentioned in the text, there is difference of opinion as to whether the similarities exhibited are significant. In these exceptional cases there is disagreement concerning the true constitution of the phyla.

[2] There is a fifth uncommon group including only a number of species of the caterpillarlike Peripatus.

must have, or must have had, some fundamental connection. The very obvious order which exists amid all the diversity of living things can scarcely be reconciled with a totally independent origin of each of the groups.

It was partly to explain this natural order that the doctrine of origin by evolution was enunciated. This doctrine made use, for all the groups in the classification, of a principle adopted by everyone as applicable to the members of a species. It has always been recognized, even by those who did not accept the idea of evolution, that the individuals belonging to one species have sprung from a common ancestry and that they owe their similarities to inheritance of the ancestral qualities. The principle of descent was used in the oldest taxonomies when males and females very different in form were included in the same species; or when queens, workers, and drones among bees, or winged, wingless, and gamic aphids were considered single units in classification. If the same reasoning be applied to groups of higher rank, it should be concluded that the species belonging to a single genus have likewise come from common ancestors. In like manner, the genera that are nearly enough alike to be included in one family must, if the principle of similarity due to common inheritance be applied, be supposed to be descended from ancestors common to them but different from the ancestors from which the genera belonging to other families were derived. So also the families of each order must belong to a different line of descent from all families belonging to any other order. All orders composing one class must have had different ancestors from all orders constituting any other class. And so on to the classes of each phylum.

The branching nature of the classification is diagrammatically shown in Fig. 17. In this figure the living world is confined to the periphery of the diagram; the central area represents only its genetic connections. The short radial lines at the periphery represent species, and the distances between these lines indicate the extent of the differences between species. The groups of one to six lines (species) placed close together constitute genera. The two to five genera close together, but separated from other genera by wider gaps (greater differences), are the families. The two or three families placed near one another constitute an order; there are only four of these, complete, in the diagram. Finally, three of these orders, grouped closer to one another than to the other orders or fragments of orders, make up the one class represented. The diagram is not large enough to show phyla. It should be emphasized that present living things are exclusively at the circum-

ference of such a diagram, grouped there according to their similarities and differences. The treelike scheme of connecting lines indicates the concept of kinship which would explain the degrees of likeness.

The assumptions regarding common ancestry are made because no phenomenon of life other than heredity is known which would account for the observed similarities among groups. They entail evolution as a corollary, however, because there are also differences among the similar groups. If several species have sprung from the same ancestors,
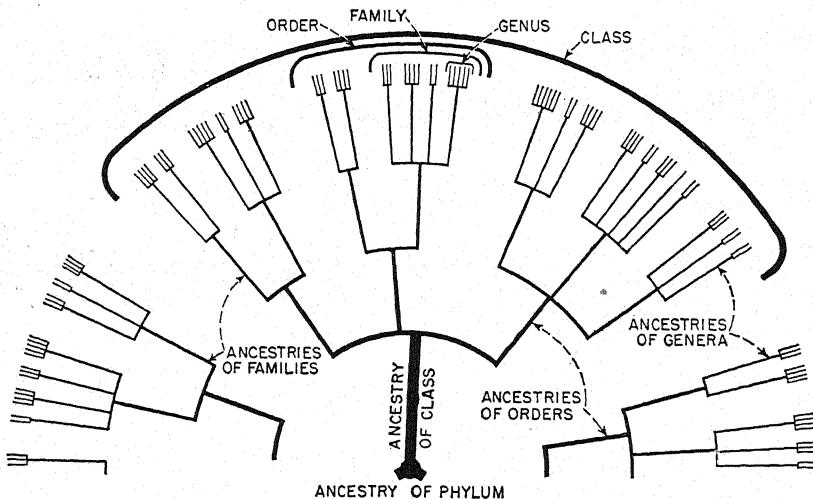
FIG. 17. Diagram of the branching nature of classification, representing one class and parts of two others, all greatly contracted.

their differences must have originated somehow in contravention, or as an alteration, of heredity. If numerous genera are descended from the same source to make a present-day family, inheritance must somewhere have been modified to bring about the differences between the genera. If it be assumed that descent may here and there involve modification, it would be expected that living things today would be capable of a branching arrangement, with branches divided and subdivided, that is, they would fall into groups within groups. The branching nature of the classification of animals and plants was observed before evolution was conceived. It was one of the incentives to the adoption of the evolution theory and is one of the potent reasons for recognizing the truth of that theory.

To avoid confusion it should be pointed out that, in assuming different ancestries for different groups, the time at which the ancestors

in question lived is an important consideration. If all vertebrate animals (part of the phylum Chordata) have descended from common ancestors, then two genera of mice have these ancestors in common; also the reptiles and the birds have both descended from these same ancestors. The common ancestors of all these vertebrates, however, must have lived a very long time ago. When it is said that the reptiles had different ancestors from the birds, reference is made to the most recent common ancestors of the reptiles and the most recent common ancestors of the birds. These must have been different animals, and must have lived at a time not quite so remote as did the ancestors common to the whole phylum. Likewise, when it is assumed that field mice (several species) had different ancestors from the jumping mice (also several species), it is the most recent common ancestors of the two groups to which reference is made. With this qualification, nearly always implied but seldom expressed, that it is the most recent common ancestors which are meant when common ancestors are mentioned, two or more somewhat similar groups are assumed, on the evolution doctrine, to have had common ancestors that were different from those of certain other somewhat similar groups of the same rank. In general, present-day species must have had relatively recent common ancestors, genera common ancestors not quite so recent, families ancestors more remote, and so on.

Age of Groups of Different Ranks. From the above considerations it is obvious that on the average species at the present time are younger than genera, genera younger than families, orders younger than classes. It is probably not true that all present species are younger than all genera. A rapid succession of changes in one branch of the tree of descent might well lead to the amount of differentiation appropriate to half a dozen genera, each divided into several species, and all belonging to one family, while in the same period of time in another branch of descent relatively few changes would have given rise only to three or four species. In this situation some of the genera of the former line might be younger than some of the species of the latter. There may well be many instances of such unequal rates of change. Nevertheless, it could hardly be otherwise than that on the whole species are younger than genera, genera younger than families.

While these statements are probably true regarding species, genera, families, etc., as concrete assemblages of living things at the present time, they should not be true of species, genera, and families in the abstract. Species as a category, without reference to any particular species, must be the oldest of all the taxonomic groups, phyla the

youngest. For, if life originated but once, and the descendants of the primeval organism inherited all the qualities of their first ancestor without change, there was at that time only one species. When a change occurred and was transmitted to a group of individuals, two species were then in existence. It was not until one or more of these species became further differentiated into species and, in their change, had diverged somewhat from the other groups of species being formed at the same time, that anything like a modern genus would arise. With further differentiation, a genus could become a family, each of the former species of the genus becoming, perhaps though not necessarily, a genus of the family. Differentiation must have proceeded far before groups complex enough to compare with present orders or classes would be produced. Phyla would be the last to be formed, and hence, as a category, the youngest.

If the above suppositions are correct, evolution of all the groups has been brought about by the origin or modification of species. A genus is evolved by the splitting of a species into a group of species. A family arises by the breaking up of some or all of the species of a genus into new species. An order is produced when some or all of the species composing a family differentiate into groups of species; for this differentiation should entail a divergence of the species belonging to different genera so as to produce groups of the rank of families. So in the larger groups, it is everywhere by the origin of species out of other species, or by the modification of whole species without breaking up if that be possible, that groups of low rank are converted into groups of high rank—orders into classes, classes into phyla. Evolution in general is thus the origin of species.

Nature of Species. What, then, is this assemblage called the species? Classification has been discussed in this chapter as if it were a very simple matter. It is, on the contrary, very difficult. Every biologist has a very general idea of what he means by orders, families, genera, and species. Those who engage directly in taxonomic work doubtless have a more definite idea of the content of the various groups than do biologists in general. Unfortunately, however, taxonomists very often disagree. They are often of different opinions whether a genus consisting of two groups of species separated by a slightly wider gap should be two genera or one. In a species not all individuals are alike. Their differences may be hereditary ones, and the differentiating hereditary characters may be possessed by considerable numbers of individuals. Should these types be recognized as two different species? There are generally accepted rules involving the distribution of the differing

types—a general topic relegated to a later chapter—but taxonomists disagree as to whether the distributional specifications have, in a given instance, been met. Some biologists make two species where others would be content with one. Some recognize subspecies—a category not mentioned in the general scheme because not all species are thus divided—where others regard such separation as unwarranted. Other uncertainties in taxonomy concern the allocation of a given species to this or to that genus, when it is almost equally similar to the species of both genera. The same difficulty arises in the allocation of genera to families, and sometimes in the arrangement of even higher groups. That these difficulties are real and frequent is shown by the number of times classifications have been changed, in each of the respects indicated, by different taxonomists.

Only an approximate and somewhat generalized idea of a species can therefore be given. It is a group of individuals most of which possess most of their qualities in common. It differs from all other groups of individuals in one or more respects, usually readily recognizable. Intergrading forms between two species are not common, relatively speaking, so that the separation of species is for the most part rather sharp. There is a strong tendency for different species to occupy different regions. While there may be overlapping of ranges, it is rare that two ranges coincide at all boundaries. It is particularly worthy of note that species differing only slightly are prone to be geographically almost entirely separate, though usually adjoining. There is usually some degree of sterility between species. While some species cross freely and produce fertile hybrids, it is much more common either that two individuals of different species are incapable of producing offspring or, if they produce offspring, that these offspring are partially or wholly sterile. Species show a high degree of permanence; that is, over a long period of time members of a line of descent possess largely the same characters. Nevertheless, there is much evidence to show that species possess plasticity; that is, they are subject to a certain amount of change in the course of many generations.

These are the characters of species—similarity of their individuals, difference from other species, infrequency of intergrading forms, a tendency to occupy different regions, the frequency of interspecific sterility, a considerable degree of permanence, and a certain amount of plasticity. It will be necessary to refer to all of them in the discussion of evolution in later chapters.

Adaptiveness of Taxonomic Distinctions. To many naturalists the fitness of living things to the situations in which they live has seemed

the most remarkable thing about them. To all of them, probably, adaptation has appeared to be greater than could be accounted for by mere chance. Doubtless an exaggerated notion of the fitness of animals and plants exists and has long existed; many special features regarded by some naturalists as adaptive probably have no use at all, and other features which are of use are not at all essential to the well-being of their possessors. Nevertheless, after making allowance for mistaken inferences, the nice adjustment of the structural and physiological properties of organisms to the environment is truly remarkable.

This adaptation is very unequally distributed through the several taxonomic ranks. In general it is considerable in the high ranks, slight or wanting in the low ranks. The class of fishes is plainly adapted, by the possession of fins and gills, and by their characteristic body form, to an aquatic habitat. Birds (with some exceptions) are as obviously adapted to aerial locomotion. In none of the other classes of vertebrate animals does any such distinctive adaptation extend throughout the group, and in almost none of the classes of invertebrate phyla is the adaptive relation so simple and extensive. Among orders, to consider only mammals because they are popularly well known, the group of bats is strikingly adapted to flight, and the seals and walruses, also the whales, and the sea cows, to aquatic life. These are conspicuous adaptations because other mammals are confined to the surface of the land or to trees. The rodents (an order) lack canine teeth, but have continuously growing incisor teeth, which they use for gnawing. The marsupial mammals (an order) possess ventral pouches, an adaptation to protection of the young, which are exceptionally immature at birth. Among families, the moles are adapted to burrowing, the opossums to life in the trees, the beavers to a semiaquatic existence, while the porcupines are exceptionally protected by their quills against enemies. It should be understood that not all differences between groups of these higher ranks are so adaptive as these; the ones named are outstanding examples of usefulnes. There are some class, ordinal, and family distinctions which are not obviously and markedly useful to their possessors. The probable reasons for the existence of both adaptive and nonadaptive taxonomic differences will appear in a later chapter.

When one descends to genera, it is much more difficult to point out the adaptive significance of the distinguishing features. The panthers and jaguars constitute one genus (Felis), and the lynxes and bobcats another genus (Lynx), the only North American genera of the cat

family. One of the differences between them is that the former group have one more upper premolar tooth on each side than the latter. It is almost inconceivable that this difference is of any functional significance in the lives of these animals. There are other differences between the two genera, size being one of them. The panthers and jaguars are larger than the lynxes and bobcats, and advantage is taken of their larger size by the former to pursue larger game (deer and sheep, as compared with rabbits and smaller mammals taken by the lynxes). But the adaptive significance of size is small compared with that of the family characters possessed by both of these genera—their lithe muscular bodies, sharp, retractile claws, and the shearing (non-crushing) form of their teeth in general. Obviously adaptive generic characters are those of the muskrats (genus Ondatra), particularly their broad feet, the hind ones partially webbed, their dense water-proof underfur, and their laterally compressed tails. With these characters, it is not surprising to find muskrats always near water and preferring swimming to locomotion on land.

In the known difference between two similar species it is usually impossible to see any adaptation. In the mammals, such differences often involve chiefly color or size and are slight. Two species of chipmunk differ by less than 10 per cent in size, and the outer stripes of one are less conspicuous than those of the other. Two species of white-footed mice differ mostly in shades of color; their size is nearly the same. Of two porcupine species, one has hairs tipped with yellowish white, the other tipped with greenish yellow, and the latter is a little smaller. One hare has grayish to buffy-brown pelage, its feet gray on top; another hare is reddish brown with more reddish feet and is an inch shorter. These examples will suffice. In all the animal kingdom, such differences between species can be duplicated with respect to their functional insignificance. Indeed, it is hard not to duplicate them. One rarely finds that the observable difference between two species of the same genus is advantageous to either one. Naturalists have sometimes pointed out that man's inability to see the usefulness of these distinctions or to detect the more significant physiological differences may only be a result of his dullness of perception and understanding. This comment is usually designed to remove a stumbling block in the way of a particular theory of evolution. As an argument it is two-edged, however. If we are to decline to recognize lack of adaptation because of our ignorance, we should be as ready to acknowledge that some things that look adaptive to us really are not so. This latter attitude would doubtless have saved more false

steps in evolution theory than the former. It is a more logical procedure to accept the evidence as it appears, and attempt to discover what it means, rather than argue it away.

Taking the evidence regarding the adaptiveness of taxonomic distinctions at its apparent value, one must conclude that the characters of the higher ranks (classes, orders, families) are often, perhaps usually, adaptive, those of genera less often or less certainly so, while known specific distinctions are usually not adaptive. If the origin of the groups is what the classification itself suggests it to be, species arising first and gradually evolving into the higher and higher groups, it means that adaptation lags behind evolution. This has an important bearing upon at least two evolution theories to be discussed later.

LIKENESS IMPLYING KINSHIP

> There can be but one perfect method of [classification], which is the natural method . . . each being is determined by its resemblance to others, and difference from them.
> —BARON CUVIER, 1828

The similarities in accordance with which animals and plants are grouped in a classification have been alluded to in the preceding chapter mostly in very general terms. The taxonomic groups were illustrated with animals so well known and so obviously similar within the groups but different as between groups, that descriptions of the similarities and differences were unnecessary. It was only in connection with possible adaptations that concrete examples of distinguishing characters were mentioned. To convey to "nonbiological" readers an adequate notion of the grounds for attributing such resemblances to heredity and hence to descent from common ancestors, it seems desirable to enumerate or describe some examples. The study of zoology and botany, especially the branch of comparative morphology (or anatomy), is replete with them. Indeed, in so far as these sciences deal with classification, the characters possessed in common constitute their entire subject matter. Reference can be made here to only a few such characters.

Taxonomic Characters. The characters most obviously useful for delimiting taxonomic groups are those possessed by only one group, lacking in all others of the same rank. Among the phyla, the group to which the jellyfishes, hydroids, and sea anemones belong (coelenterates) is thus distinguished by stinging cells (Fig. 18); every coelenterate possesses these organs of attack and defense, and no other phylum has them. The phylum of sponges has, within the passages through which water circulates, layers of cells each having a flagellum surrounded by a collar (Fig. 18); no other phylum of multicellular animals has such collared cells, though certain of the single-celled

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organisms have collars. Only one phylum has a horny skeleton on the outside of the body; that group (arthropods) includes the insects, crustacea, spiders, centipedes, etc. The only phylum possessing an internal skeleton of bone is that of the chordates (fishes, amphibia, reptiles, birds, mammals); but within this group are some forms which do not have a bony skeleton. This same phylum also has its central nervous system above or dorsal to the digestive tract, while in all other phyla the nerve cord is chiefly ventral in position.

Some characters are possessed by two or more phyla; in such cases there are other features which distinguish the groups. The coelenter-
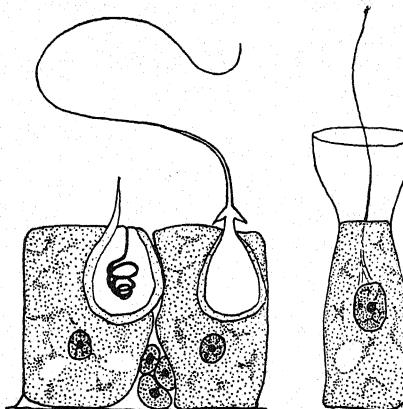
FIG. 18. The distinguishing marks of two phyla. *Left,* two stinging cells, one of them discharged, lodged among other cells of Hydra, the marks of a coelenterate; *right,* a collared flagellate cell, found only in sponges among multicellular animals.

ates have only two layers of cells in their body walls, but so also do the sponges; these two groups are then distinguished by the collared cells, water pores, and horny or needle-framework skeleton of the sponges, and the stinging cells of the coelenterates. The coelenterates have only one opening (the mouth) in their digestive cavity, but a cavity of this kind occurs also in the flatworms; the flatworms, however, do not have stinging cells and have bilateral symmetry, whereas the coelenterates are radial. A simple type of excretory system in which the primary function is performed by a "flame" cell, a hollow cell in which the excretions are moved along by the undulations of a flaglike structure, is found in both flatworms and rotifers; but these phyla are very different in most other respects.

Groups of lower rank are similarly marked. One class of mollusks (the snails) has a spiral shell (if any shell at all), another class has

a shell composed of two hinged valves which open and close like a book (clams, oysters), while a third class has arms bearing suckers (cuttlefishes). All members of the class crustacea (crayfishes, barnacles, etc.) respire by means of gills, even though some of them dwell on land; three other classes of arthropods (insects, centipedes, and the caterpillarlike Peripatus) introduce air by fine tubes penetrating all parts of their bodies. These three latter classes have their distinguishing characters which need not be described.

Orders are distinguished in similar ways. Insects regularly have four wings; but the Diptera (flies) have only two, the hind pair being replaced with club-shaped balancers. In most insects having four wings, both pairs are used for flight; but in all beetles the front wings are hard covers which in flight are merely elevated to make room for the second pair to beat and at rest serve to protect the hind wings. Butterflies and moths all have on their wings shinglelike scales in which the color patterns are developed; some other insects have hairs or spines on the wings, but nothing like scales. Several orders of insects have sucking mouth parts (bugs, thrips); other orders bite (grasshoppers, beetles, dragonflies); the orders that are alike in this one respect are, of course, different in a number of others. Striking similarities and differences are also found in the type of development. All insects of the several orders to which grasshoppers, bugs, and dragonflies belong undergo a development in which each stage molts its skin to form a larger animal differing from itself only slightly in structure. Butterflies, beetles, flies, and bees, on the contrary, pass through three radically different stages—larva, pupa, adult—so unlike in structure that the uninitiated would suspect no connection between them.

These examples must suffice for taxonomic distinctions of the higher ranks in general. Were the entire animal kingdom surveyed, from phyla down to orders, even with no more minute analysis than that given above, almost the entire subject matter of a second-year course in zoology or comparative anatomy would be involved. To extend the same analysis down through families, genera, and species, with their increasingly smaller differences, would draw upon scores or hundreds of specialized works, often of large size. The advantage of such analysis would be too small to compensate for the labor. To the vertebrate animals, however, chiefly because their organization is similar to that of man and is consequently more or less familiar, it is worth while to turn for further illustrations.

Vertebrate Taxonomic Characters. If certain groups be omitted from consideration, the vertebrates are characterized by an internal bony

skeleton, a hollow nervous system located all on one side of the digestive tract (usually to be described as the upper or dorsal side), and gill slits opening from the throat to the outside or touching the outside wall in at least the developmental stages. These characters are found in no other phylum. In the fishes, the gill slits persist throughout life, and between them the gills are developed as respiratory organs; the limbs are in the form of fins; the skin usually contains scales; and the heart consists of only two chambers. In the amphibia (frogs, toads, salamanders), gills are present and functional in the larval or tadpole stage, and in some kinds they persist throughout life. The amphibian skin is devoid of any hard structures, and the heart has three chambers (two auricles and one ventricle). The reptiles never have gills in any stage, and the gill slits are open only in the embryo; in this respect they are like birds and mammals. The heart is generally three-chambered, though the ventricle is partially divided, and in crocodiles it is completely divided so that the heart is four-chambered. The body of a reptile is covered with scales or hard plates. Birds possess feathers, wings (functionless in some), a four-chambered heart, and air cavities in some of the bones and are devoid of teeth. Mammals have hair, a diaphragm separating the chest from the abdomen, and a four-chambered heart. Embryonic development of mammals takes place as a rule within the body of the female, and the young are nourished with milk. The fishes, amphibia, and reptiles are cold-blooded, while birds and mammals are warm-blooded.

Similarities Emphasized. The vertebrate characters which remain to be described are not advantageously referred to as taxonomic distinctions. Instead of pointing out the differences among various animals with respect to them, more is to be gained by emphasizing their similarities. The brain is an example. While some brains are long and narrow, others short and wide, some flat and others high, they all possess the same principal features. Cerebrum, cerebellum, optic lobes, pituitary body, and the crossed optic nerves are readily discernible notwithstanding their variable forms.

The nerves that emerge from the central nervous system within the skull show likewise great similarity. They arise from the same part of the brain, and most of them pass to the same organs and serve the same function. The first of these nerves, counting from the front, is the nerve of smell, the second is the optic nerve, and the eighth is the nerve of hearing in all vertebrate animals. The third, fourth, and sixth are distributed to the muscles which move the eye. The remaining cranial nerves—there are 10 of them in the lower vertebrates, 12 in the higher

—go to various regions of the face, throat, and organs of the chest, and among them there are some differences in both distribution and function in the several vertebrate classes.

The highly developed sense organs show equally great similarities. In the eye there is in all the same general arrangement. The eyeball may be of somewhat different shapes, but the transparent cornea in front, the iris and pupil, the lens, the retina, and the choroid and sclerotic coats are present and in the same general relations to one another in all of them. The inner division of the ear, to which the nerve of hearing is connected, consists of an irregularly shaped body and three semicircular canals, set in three different planes roughly perpendicular to each other. Each canal of this membranous labyrinth has an enlargement near one end in all the classes of vertebrates described above. From the frogs to the mammals, there is, adjoining the membranous labyrinth, a cavity known as the tympanum, which is connected with the throat by a tube, and in which in all these classes are small bones which serve to convey the vibrations producing sound.

Any other system of organs could be used for similar comparisons and would yield the same conclusions. Digestive systems in the bulk of the vertebrates consist of corresponding organs in the same order, with the appropriate glands pouring secretions into them at the same places. Excretory systems consist largely of the same mechanisms; muscles are arranged in much the same ways, are attached to corresponding bones, and serve mostly the same functions; blood vessels follow the same general courses, give off branches usually at the same points, and serve the same portions of the body. It might be argued that these systems, in order to perform their functions, must be arranged in these ways, and that the fact that they are so much alike in the various vertebrates means only that they have certain things to do in relation to each other and are situated in the only places where these things can be done. This argument could not be applied, however, to the location of the endocrine glands (Fig. 19). These organs produce secretions which, instead of being poured out through ducts, diffuse directly into the blood. In this liquid the secretions are carried everywhere, and there would be no necessity of having the glands located at any specific points. Yet the thyroid gland occurs always in the region of the throat near the front gill slits, from which place its secretion flows out to influence physiological processes in the remotest parts of the body. The pituitary, located always at the base of the brain, might be anywhere else and influence growth and the reproductive system equally well. The thymus develops always in the region of the gill slits, but in the

adult extends, in the several classes of vertebrates, to various places in the neck region or upper part of the chest—far from the seat of its principal known and supposed effects. The reproductive organs produce endocrine secretions which influence secondary sexual characters literally from head to foot (combs, wattles, tail feathers, and spurs of fowls, for example). The conclusion that these organs might be elsewhere and still serve the same purpose is not mere conjecture. It has
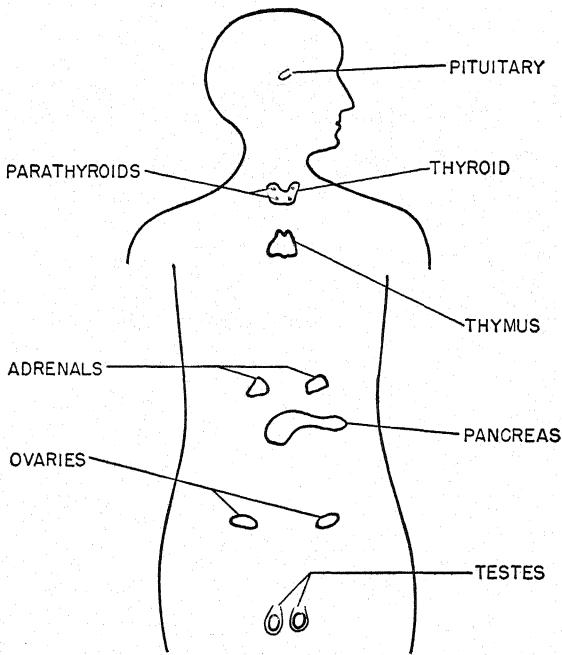
FIG. 19. Location of endocrine glands in man.

been proved by grafting them into strange situations or by introducing their secretions artificially at other points.

Internal Similarity with External Difference. If experiments with the endocrine secretions show that a given function could be performed regardless of any particular anatomical arrangement, there are situations in which the tables are turned and many different functions are performed by essentially the same anatomical structure. A classical example of this relation, often described because it extends over a large number of well-known animals, is found in the fore and hind limbs of vertebrate animals. These limbs possess very similar skeletal foundations, but are externally modified in so many ways that

they may be used for many different purposes. The human arm is
rather simple and unspecialized, and its skeleton may be used as a
starting point for comparisons. It is attached to the trunk through a
shoulder girdle composed, on each side, of a collarbone and a shoulder
blade. The upper arm consists of one bone, the lower arm of two
bones, and the wrist of a group of irregular small bones. Beyond these
there are five chains of bones set end to end to form the body of the
hand and the digits. Among the least specialized of the arms of other
vertebrates is that of the frog. Its shoulder girdle contains a third
bone on each side which forms the chief brace of the arm against the
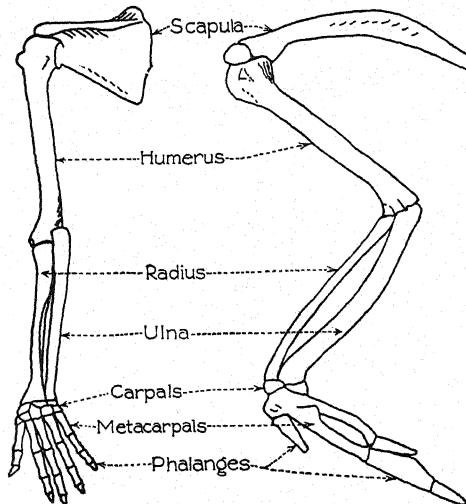
Fig. 20. Skeleton of human arm and bird's wing, showing correspondence of their
bones.

breastbone. The arm itself differs from the human arm chiefly in that
the two bones of the lower arm are fused side by side, the small bones
of the wrist are less numerous, and there are practically only four rows
of bones in the hand with somewhat different numbers of bones in
them. In the sea turtles the forelimb is externally a long flat paddle,
not divided in the flesh into separate fingers at the end. Yet, with
the exception of the inflexibility of some of the joints, the bony struc-
ture within, even to the number of segments in the digits, is essentially
the same as in many land vertebrates. The arms of whales are likewise
flat and without separation of the digits in the flesh; but their skeletons
differ from typical vertebrate arms almost only in the absence of a
collarbone, the immovability of the elbow joint, and an increase in

the number of bones in the digits. In bats, the principal modification is the great elongation of the bones of the body of the hands and the fingers (except the thumbs) to form the framework of the wings. One of the bones of the lower arm is rudimentary; otherwise the arm skeleton is typical. In birds the wing is formed, not by an extension of the digits, but notwithstanding a great reduction of them. There are only three fingers (Fig. 20), and each of these has one or two fewer bones than the corresponding fingers of man. The expanse of wing thus lost is more than compensated by very stiff feathers. The only other striking difference between the bird wing and a typical vertebrate forearm is the reduction of the separate wristbones to two. In the forefeet of horses there is only one well-developed chain of bones instead of the usual four or five, while two others are represented by the single splint bones on either side. The single toe in these animals is generally held to be in the interest of speed. In snakes the forelimbs are completely wanting, though the other skeletal characters show many resemblances to other vertebrates.

The hind limbs show somewhat fewer and less striking departures from the ordinary. In sea turtles and horses their modifications are of about the same kind and degree as those of the forelimbs. In most whales they are entirely missing, though in a few there are small bones (Fig. 21) embedded in the flesh in the pelvic region without any connection with the spinal column, which are usually homologized with the hip girdle. In most snakes, likewise, hind legs are wholly wanting. In a few (including the python and the boa), hind legs are externally visible only as clawlike structures scarcely protruding beyond the general level of the scales on the surface. Connected with these claws internally are rudimentary bones representing the girdle and probably one or more of the leg bones.

Similarities between Embryos. It is not only in adult structure that similarity exists between animals of different groups. Their embryos may show equally striking likenesses. Without inquiring at once how significant these various resemblances may be, one may point out that they exist from the very beginning of development. Throughout the animal kingdom development involved in sexual reproduction begins with an egg, either fertilized or not, and the first step in development is the division of that egg. This cleavage continues and in almost all cases results in a hollow ball of cells, the blastula. One side of this ball is turned in (in very various ways) to form a double-walled embryo or gastrula, in which, in most phyla, a third layer is soon split off or budded off.

From this point on the similarities are striking only if compari-
sons be limited to one great group, and for this purpose the verte-
brates are here selected. In all the vertebrates the nervous system
arises early from two ridges formed on the outside of the embryo and
later fused to form a tube below the surface layer of cells. From this
tube, in all vertebrates, the eyes start as a protrusion on each side near
the front end, and subsequent steps are very much the same in all.
The ears start as a depression from the outside in the head region,
resulting soon in a pear-shaped sac beneath the surface layer. This
sac forms the membranous labyrinth with its three semicircular canals
which have already been described as similar in the adult in all verte-
brates. The digestive tract exists from the moment that the double-
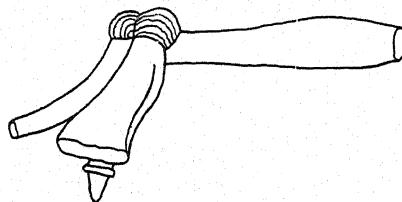
FIG. 21. Vestigial skeleton of hind legs of some whales. The bones are not attached
to the rest of the skeleton, and no leg protrudes from the body.

walled embryo is formed; it is the sac formed by the inner one of the
two layers. The gill slits arise, in all vertebrates, as outpocketings of
this inner cavity near its front end. The liver is derived in all of them
from a protrusion on the underside of this cavity just behind the en-
largement which later becomes the stomach. The pancreas is produced
by two such protrusions on opposite sides of the digestive tract. The
heart, in all vertebrates, begins as an S-shaped tube formed in the
third layer of cells toward the ventral side. The excretory organs start
as a series of tubes extending out from the body cavity; these later
come to be associated with minute blood vessels, in almost exactly
the same way in all vertebrates. The spinal column originates in all of
them as a rod of cells just below the central nervous system, around
which later cartilage is formed and eventually bone is deposited.

The Biogenetic Law. How early in this developmental process one
should look for similarities that bear on kinship is uncertain. One of
the earlier evolutionists to appeal to this type of evidence, Ernst
Haeckel (Fig. 14), started from the very beginning—the egg. This he
likened to a single-celled organism, a protozoon, and pointed out that
one or more unicellular beings must be the ancestors of the present

multicellular ones. In development, the egg cleaves and forms the hollow blastula, and Haeckel assumed that such a colonial form stood in the ancestry of all the modern forms. There now exist such blastula-like forms among the low plants, Eudorina, Pleodorina, and Volvox, for example, but none among modern animals. From the blastula comes the two-layered gastrula, also held by Haeckel to be the form of an early ancestor, and the coelenterates (Hydra) furnish modern examples of this two-layered condition. All along the path of descent represented by these organisms there entered the differentiation of the adhering cells into a number of kinds, as is now done individually in Pleodorina, Volvox, and Hydra. Leaping over a long series of events, one may note the presence of gill slits, some of them never actually open, in the embryos of all vertebrate animals, including those which do not have gills in the adult. According to Haeckel's scheme, these embryonic gill slits are remnants of gills which the adult ancestors of an early time possessed. That is, the ancestry of the whole vertebrate group at that time was aquatic and respired by gills.

Haeckel was outlining what he called the *biogenetic law*, according to which each individual in its own development repeats the changes which the race experienced. Early embryonic stages were held to represent early ancestors, late stages late ancestors, and so on. How much of this theory is valid is questionable. Certainly not all of it is. If the "law" held absolutely, all that would be needed to trace the evolution of any modern animal would be to work out its embryology very carefully. Some present-day biologists have rejected Haeckel's law because it does not do all, or even very much, of what he claimed for it. Fortunately for the purpose of this book, it is not necessary that the biogenetic law should have complete, or even very general, validity. If only it is true that embryos possess certain features as an inheritance from the past, that purpose is served. If reptiles, birds, and mammals have embryonic gill slits, or approaches to them, because ancestors had gills, these structures furnish the kind of evidence for which we have been surveying the embryonic process. Probably all biologists, whatever their estimates of the biogenetic law, regard the gill slits of mammals as homologous with those of fishes. There must be many such inherited embryonic features. Wherever they exist, embryonic likeness is put at least on a par with adult likeness as diagnostic of the taxonomic groups in which they are found.

The correspondence between different classes of vertebrate animals with respect to the development of their various organs is so close that college courses in embryology can easily be based in the main

on one type. In some, it is the frog that furnishes the main laboratory study; in some it is the chick; while in others mammalian embryos are used. What is observed in one of these applies in general to the rest, with quite as much accuracy as the facts of adult anatomy in one animal indicate what is to be expected in the adult structure of other types.

Similar Embryos and Unlike Adults. More striking because of their unexpectedness, though not more valuable as evidence, are similarities between embryos of animals whose adults are quite unlike. The gill slits of the embryos of the higher classes of vertebrates would be quite unexpected from anything in the structure or physiological activities of the adults. As an inheritance from an aquatic ancestor, however, they have a meaning. Some of the slits, and the flesh between them, have a function even in nongilled vertebrates. The Eustachian tube of man, connecting the middle ear with the throat, is one of the slits. The tonsils and part of the hyoid apparatus come from certain of the bars between slits. Most of them, however, have no function; certainly the features named could well be developed without the whole set of slits and bars.

Occasionally embryos furnish the chief, and in some cases the only, clue to the relationships of animals. This is particularly true of parasites because the adult structure of such animals is frequently so degenerate as to obscure any similarities which may once have existed. Sacculina, a parasite attached to the underside of the abdomen of crabs, is a noteworthy example because it eluded classification so long. Sacculina (Fig. 22) is a rounded pulpy mass consisting mostly of reproductive cells, and having no other structural characteristics resembling any known group of animals. When some of its reproductive cells were allowed to develop under observation until the larval stage was reached, it was discovered that Sacculina belongs to the group of crustacea commonly known as barnacles. Portunion, another parasite upon crabs, is shown by its developmental stages to be an isopod, a member of the crustacean order to which the sow bugs belong. Entoconcha, parasitic in sea cucumbers (relatives of starfishes), goes through an embryonic stage known as a veliger, of a form that is characteristic of snails. Embryos are so regularly similar in animals whose adults are similar that, when embryonic similarity is found in the absence of adult likeness, it must be regarded as sound indication of kinship, especially when the adult structure does not indicate different affiliations.

Vestigial Structures. Degeneration less extreme than that exemplified in the parasites just mentioned may result in vestigial organs. While

in Sacculina all organs represented in the embryo are lost to the adult except the reproductive organs (which show no characteristic structure), and in numerous other cases certain organs of the embryo are wanting in the adult, there are many instances of structures whose embryonic start is ordinary but whose later development is retarded. Such organs are often so much reduced that they are functionless and then are known as vestigial organs.

Examples of vestigial organs are numerous. The vermiform appendix and caecum in man start in the embryo in as conspicuous a way

Adult in crab
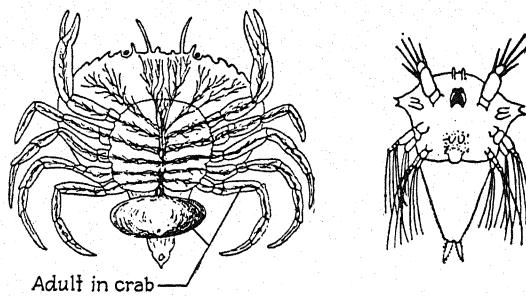
FIG. 22. Sacculina, parasitic on a crab. Its taxonomic position is determined from its larva (nauplius), *right*. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc.*)

as they do in kangaroos or rabbits, animals which in the adult stage possess these structures very well developed and presumably functional. The uselessness of the appendix in man is attested by its frequent removal without ill consequence. While surgeons sometimes hesitate to remove it in very young children because of a possible developmental function, such significance has never been demonstrated. A point of interest concerning the appendix is that it is about as much reduced in monkeys and apes as it is in man. The human coccyx consists of those vertebrae below the pelvic girdle and corresponds to the tail vertebrae of other mammals. It is much reduced in size and is immovable, though in some people rudimentary muscles are found adjoining it in the same position as the muscles that move the tail in the tailed mammals. In rare instances the coccyx is overdeveloped and produces a taillike projection. In the human embryo of an early stage it is present in as well-marked a form, the curved posterior tip of the body, as in the embryo of a tailed mammal. Ear muscles are present in man, though most people are unable to operate them. Three broad

muscles (Fig. 23) reaching from the ear to the side of the head would, if they contracted, move the ear forward, upward, and backward. Within the ear are also several muscles which would tend to alter the shape of the ear and perhaps collect the vibrations better, but they are inactive. The slender red crescent at the inner corner of the human eye begins in the embryo in precisely the same way as does the eyelid of a bird. Instead, however, of becoming functional, it is replaced by two lids of a totally different type. The cat has two outer lids, like man, but retains the use of the semilunar fold, as it is called, which may be made to sweep across the eye under the other lids. In apes and monkeys, the fold is reduced and functionless as in man.
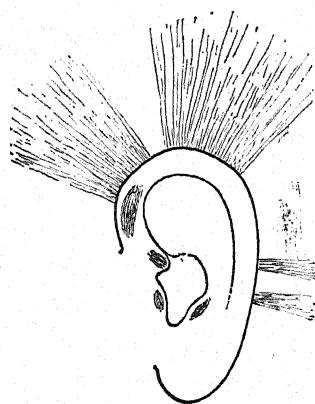
FIG. 23. Muscles that would move the human ear if they worked.

The wings of birds of several kinds suffer eclipse in the course of development. Those of the ostrich are too small to be functional, while the wings of the New Zealand kiwi are completely concealed by the plumage. In the early embryos of these birds there is no suggestion of the impending retardation of wing development. In the dodo, which is now extinct but was known on the island of Mauritius as late as the year 1681, the wings were correspondingly reduced; and in the moas of New Zealand, which are known only from recovered bones, no wing bones have ever been found. In these latter two birds there is no evidence regarding the embryonic development of wings.

The hind legs of whales are missing, except for small bones (Fig. 21) in some of them wholly embedded in the flesh and unattached to the spinal column. So inconspicuous are these bones that laboratory skeletons of whalebone whales, which are the kind that have the vestigial legs, are sometimes missing because the preparator unwittingly discarded them with the flesh. The forelegs are properly constructed arms, but small, so that they serve mostly for guidance; the powerful propulsion of the whales is furnished by the large tail flukes. A few snakes have corresponding remnants of hind legs. The splint bones at the sides of the feet of horses recall the ancestral condition in which there were at least four toes, according to the fossil evidence described in another chapter. These splints correspond, in the forelegs, to the

second and fourth metacarpals of the human hand. The one functional finger of the horse is the third, numbered from the thumb side. In the embryo the usual five digits start.

Hundreds of such vestigial structures are known. They are not any better as evidence of kinship than are well-developed homologous organs. They effectively dispose, however, of any supposition that embryonic development proceeds directly by the shortest route from the egg to the adult form. This is important in the interpretation of embryonic likeness, since it cannot be maintained that embryos are alike merely because development has to arrive at somewhat similar end products and must run everywhere the same course in order to do so.

Similarities of Physiology. Knowledge of physiological properties suffers from the fact that usually it can be gained only from experiments. To the extent, however, that physiological processes have been tested in different kinds of animals, likenesses as striking as those of structure have been found. Such studies have been made extensively in vertebrate animals because of the light they throw on human physiology, so that many comparisons are available. This knowledge will be introduced only sparingly here since much of it does not constitute "new" evidence. That is, little would be gained by reciting what the facts of physiology indicate regarding the kinship of animals where they parallel the evidence from anatomy. The organs of the digestive tract produce in the main similar enzymes in various vertebrate animals. The parts of the central nervous system perform, so far as they have been adequately tested, approximately the same functions. The nerves not merely are distributed to the same parts of the organism in different vertebrates, but serve chiefly the same ends. The functions of these organs must be in part determined by their structure and relation to other organs. Thus, an efferent nerve probably differs little in fundamental function no matter to what organ it leads; but the end result of its activity varies greatly according as it innervates a muscle or a gland. A voluntary muscle presumably contracts by means of the same physical and chemical properties no matter where it is located; but the movement effected by it depends on the bones to which its ends are attached. In this sense, and to this extent, physiology parallels anatomy and furnishes no new evidence regarding homology.

There are some physiological properties, however, which are not obviously associated with or dependent upon anatomy. Similarities between different animals with respect to such qualities should possess all the value as new evidence that an independent anatomical feature of the adult or embryo would possess. Such physiological properties

may be discovered in the blood. This statement does not refer to the similarity of the blood cells, the hemoglobin content of some of them, or the chemical composition of the blood as ascertained by ordinary chemical analyses. Such similarities are indications of kinship but are omitted because each of them can be discovered by essentially structural studies. The properties which possess evidential value of an independent sort are those revealed by serological tests.

Blood Sera. By repeatedly injecting into the blood stream of one animal the blood serum of a different kind of animal, containing strange proteins or polysaccharides, the blood of the former may be gradually rendered immune to the latter. This is done by the production of antibodies, substances whose molecules are made to take on a complementary shape which fits them to the protein or polysaccharide molecules which they are to neutralize. The presence of the antibodies is shown by the production of a white precipitate when the serum of the immunized animal is mixed with serum from the kind of animal to which it is immune. The antibodies fit best the molecules of the protein, let us say, in relation to which they were formed. If sheep serum is injected several times into the blood vessels of a rabbit, the antibodies formed in the rabbit blood fit the sheep proteins better than any other kind of proteins. So, if sheep serum is mixed with antisheep serum from the rabbit, a rather heavy flocculent white precipitate is formed. The proteins of goat serum are somewhat similar to, yet different from, those of sheep serum. If goat serum is mixed with antisheep serum, there is enough correspondence between the antibodies and the goat proteins to throw down some precipitate, but not as much as when sheep and antisheep sera are mixed. Any other serum may be mixed with antisheep serum; how much precipitate is formed depends on how nearly alike the proteins of the new serum and those of the sheep are—the more similar these proteins are, the more precipitate is produced.

The likeness of blood proteins of various animals can be ascertained on any desired scale. To compare many kinds of serum with that of cattle, it is necessary to obtain antibeef serum. To compare different bloods with that of man, one must obtain antihuman serum. In every comparison, much precipitate indicates close similarity, little precipitate small likeness, of the proteins of the two sera. The amount of the precipitate may be determined objectively by a device measuring the turbidity of the mixture, or the greatest dilution of the serum which will still produce a precipitate may be used as the measure of the extent of precipitation.

Among the many animals whose sera have been studied are some whose anatomy indicates that they are very closely related. In general, their bloods have also been found similar. Animals whose structure puts them far apart in the classification have in general shown little similarity of their serum proteins. Human blood has no close similarity to that of any other vertebrate except in the group of primates. Within the primate group, human serum is most nearly like that of the anthropoid apes. The apes are followed, with lesser degrees of similarity, by the Old World monkeys, the New World monkeys, and the lemurs. Egyptian mummies give about the same serological reactions as does modern man.

Many precipitin tests have been made in other groups of animals. Boyden and Noble have illustrated the results of comparison of four genera of salamanders by the model shown in Fig. 24. The lengths of the rods connecting the polyhedra represent the degrees of relationship among the salamanders, a long rod meaning distant relationship, a short rod close kinship. Amphiuma, Siren, and Necturus are rather closely related to one another, while Cryptobranchus is distant from all of them. Cryptobranchus has long been regarded, on anatomical and other grounds, as a primitive form. Thus the serological tests are in agreement with the morphological evidence.

FIG. 24. Model of the degrees of kinship of four salamanders, Amphiuma (A), Siren (S), Necturus (N), and Cryptobranchus (C), as determined from blood tests. (*From Boyden and Noble, American Museum Novitates.*)

Moths of different genera and subfamilies of the Phalaenidae show about the same degrees of likeness in the proteins of their body fluids as in their structure. Frozen mammoths give serological reactions much like those of living elephants, which belong to the same genus with the mammoths. Plants also would be classified in roughly the same way on the basis of their proteins as on structural comparisons. For example, the common cereals fall into two groups, one of them comprising wheat, rye, durum, and emmer, the other including corn, teosinte, kafir, and sorghum. This is the way these plants were grouped by taxonomists who knew only their structure.

Conclusion. What inferences are we to draw from the facts here narrated? In all the instances related in this chapter, similarity can be reasonably attributed to only one cause, namely, heredity from a common ancestor. Whether the likeness be exhibited in adult structure, in embryonic structure or processes, or in physiological properties, there is no other known way of attaining it than by community of descent. Such resemblances are more impressive if they are independent of other parallelism or if they occur in unexpected places but are not then necessarily of greater value as evidence. Their greatest testimonial worth lies in the fact that everywhere they point to the same conclusion.

The likenesses are thus not *direct* proof of evolution; what they show is kinship. The next step, however, is a short one. If there were no evolution, all organisms descended from the same ancestors should still be alike. There would be among them no separation into species, genera, and families. Since these differences do exist, along with the similarities, change must have occurred somewhere along the lines of descent.

CHAPTER IV

GEOGRAPHIC DISTRIBUTION AND THE TIME AND PLACE OF ORIGIN OF SPECIES

> . . . the science of geographical distribution depends essentially on a belief . . . that all animals are genetically connected one with another, and that the existing forms have originated from earlier kinds by some mode of evolution.
>
> —R. LYDEKKER, 1896

While animals and plants must live in regions to which they are suited, no species exists in all the places on the earth where the conditions are right. Indeed, many of them are not now in the best places; their situation would be improved if they could go elsewhere. The limitation of a species to areas of a certain kind is a matter of physiology. The fact that not all areas of that kind are occupied by the species must be historical; the species has not had time, or has not been able, to move into the other favorable situations.

These observations are valid regardless of the manner of origin of species. They would be as true if species were independently created as they would be if species arose by modification of some individuals of other species. It must be remembered, however, that the earth, as a place to live, has itself experienced many changes. It has undergone an evolution. If species of animals have also arisen by evolution, it is almost inevitable that the two evolutions should intertwine. What the earth was doing at the moment when a new species was getting under way could have a profound influence on the fate of the new species. Almost certainly the distribution of species in general would show some peculiarities in relation to the earth's history. Now, if there are peculiarities of distribution, and these are intelligible on the supposition that species have evolved but are meaningless on any other theory, the facts of distribution are circumstantial evidence of evolution. There are many such situations, some on a continental scale, some relating to small areas. We shall examine some of these peculiarities. In dealing with continental questions it will be necessary

to refer to fossils and other geological evidence, which are the sub-
ject matter of the next chapter, but the needed foundation can be
made intelligible.

   The Western Continents. North and South America differ very
markedly in their large mammals. One of the contrasts is the existence
of members of the camel family in the southern continent, not in the
northern. One must ignore the domesticated forms, for in a much-
traveled world these animals may be taken anywhere. The only other
continent to contain wild members of the camel family is Asia. There
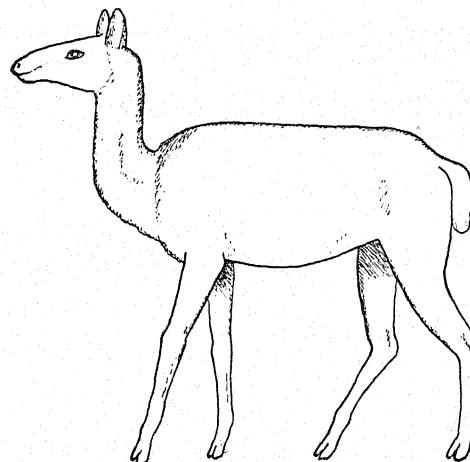
FIG. 25. The first camel, Poëbrotherium, from the badlands of western United
States.

they are the true camels, while in South America they are the guanacos
and llamas. Now, fossils show that for a long time in the Tertiary
period camels existed only in North America (Fig. 25); there were none
anywhere else. Late in Tertiary, however, they existed in both South
America and Asia but were of different kinds in these two areas. The
latter continent has been repeatedly connected with and separated
from North America across the Bering Sea, so that exchange of animals
has often occurred. Then all the family died out in North America.

   These are the facts: camels only in North America at first; then
camels in two continents adjoining North America; different kinds of
both fossil and living camels in those two continents; and no camels
at any time in other continents. The evolutionary explanation of these
facts is that camels arose in North America, evolved in several dif-
ferent ways, migrated to such places as had land connections with

their place of origin, then died out in their first home. It would be difficult to devise any rational explanation of their distribution not involving evolution.

Two Groups of South American Mammals. The loss of the camels of North America was part of a catastrophic destruction of most of the great mammals soon after the appearance of man—a general extinction which has never been explained. This annihilation of the great, highly developed mammals has left, in South America, two rather distinct groups of species. First, there are the anteaters, sloths, and armadillos, which are regarded on anatomical grounds as primitive; many opossums and another marsupial (pouched mammal) similar to the marsupials of Australia, all primitive; the platyrrhine (including the prehensile-tailed) monkeys and the marmosets, which are among the more primitive primates; and a number of odd rodents (including the largest member of that order in the world) not found in any other continent. This is one of the groups mentioned—peculiar to South America and on the whole primitive. Dwelling with these distinctly South American mammals is the second group, comprising forms more like those of the north. Among these are the tapirs, guanacos and llamas, deer, cats, wolves, otters, and numerous rodents. They are not at all primitive types. Though mostly they are of different species, and often of different genera, from those of North America, yet there is a plain likeness of this group to the northern mammals. Here is a peculiar distribution—a group of primitive mammals practically limited to South America, and a group of higher forms found in both northern and southern continents.

The Submergence of Panama. On the supposition that mammals have evolved, this odd distribution has a simple explanation. Certain fossils found on land in Panama are of marine types, similar to forms which elsewhere have been allocated to Miocene (mid-Tertiary) time. This means that Panama was then submerged, and North and South America were separated (Fig. 26). Before the marine fossils of Panama were discovered, students of the fishes that live on the two sides of the isthmus had concluded that the connection of the two continents must have occurred about Miocene time.

Thus, at a time when, on the evolutionary hypothesis, all mammals were still rather primitive, South America was developing its own peculiar types, secure from invasion from other parts of the world. Then when Panama rose out of the sea, connecting the two continents, exchange of land animals could begin. North America had by this time developed its own kinds of mammals which resembled the Old

World forms, presumably because of the frequent land connection across the Bering Sea. The earliest of these northern forms to go across the isthmian bridge, so far as known, was a raccoonlike carnivore. The earliest known migrant north from South America was a ground sloth. These early migrants are both extinct; both were of Miocene time. They were followed by many others, going in both directions. The northward migration was not very fortunate, and most of these migrating forms became extinct. The Canada porcupine is a remnant
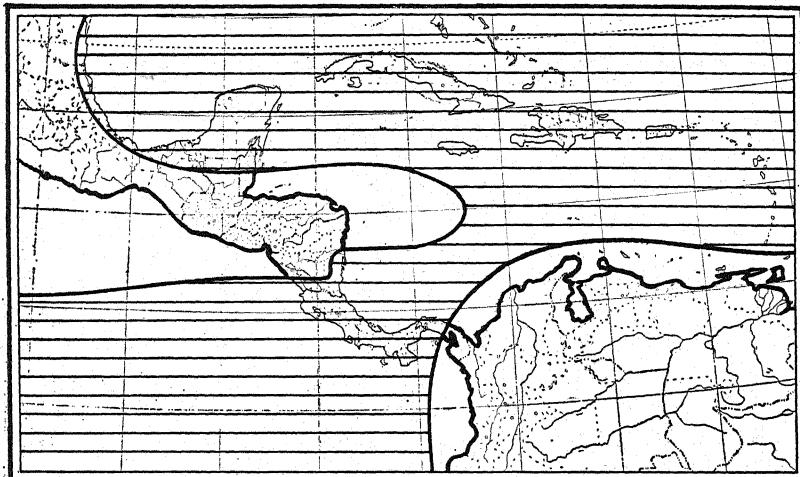
FIG. 26. Separation of North from South America at Panama in Oligocene, continuing into Miocene. Shaded area, ocean.

of it, and North America's one marsupial, the opossum (Fig. 27), is generally regarded as part of the northward immigrant invasion. The southward migration was more successful. Among these North American types are deer that went as far as Chile (the brocket) and Argentina (the pampas deer), and these are considerably modified from northern deer types. Deer that arrived later and have gone only as far as the Guianas are still much like those of Florida. The skunks, bush dogs, and wolves are similar to those of the north. Among the southward migrants are some that became extinct—the saber-toothed tigers, short-faced bears, mastodons, horses—but their disappearance was part of the great extinction of mammals already mentioned and affected North America as well.

It is scarcely conceivable that these differences in the faunas of the two Americas could arise out of a creational origin of species. Totally

independent origins of these forms could hardly have resulted in such an interrelated group of products. The fact that, with an origin of species from other species, the peculiarities of American distribution have a consistent and harmonious explanation is strong support for such evolutionary origin.

Primitiveness of Southern Faunas. The existence of many primitive mammals in South America is but part of a general condition affecting the other southern continents. To say that a given fauna is more primitive does not mean that all the animals are primitive, merely

Fig. 27. American opossum, immigrant from South America. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc., photograph by D. R. Dickey.*)

that among them are more numerous primitive types than elsewhere. Australia is notable for the prevalence of monotremes and marsupials, both primitive mammalian groups. Among the higher mammals the dingo and the rabbit have been introduced, the former probably, and the latter certainly, by man, and both are doing very well for themselves. Australia also has some of the most primitive insects of three orders—the bees, termites, and the butterflies and moths. One of the three genera of lungfishes is likewise Australian (Fig. 28). Much of Africa is unknown, but south of the Sahara are a number of primitive types. There are the small deerlike chevrotain of West Africa, the lemurs (most primitive primates), the aardwolf, the golden mole, and another genus of lungfishes. In Africa's major island neighbor, Madagascar, are a host of lemurs, and the most primitive bird of the crane and rail group. In South America, besides the primitive mammals already mentioned and a third genus of lungfishes, are primitive land

snails. Indeed, the snails and other mollusks of all the southern continents are more primitive on the whole than those of the north.

History of the Mammals. The primitiveness of the southern faunas has led to a widely accepted theory of the origin of the mammals. According to that theory the earliest mammals appeared in the northern land mass, either Eurasia or North America. One fact and one bit of speculation are the primary foundation of this theory of the place of origin. The fact: that the earliest fossil mammals, of the monotreme or marsupial type, have been found in Asia—a fact weakened by the more intensive paleontological study of the northern continents. The speculation: that a great land mass is subject to the more variable climatic conditions which would stimulate evolution of a new group. These early northern mammals spread over the world, in all directions. They could not go far to the north before striking impossible climate, but the path south was open all the way to the tips of Africa and South America and through Australia.

FIG. 28. Lungfishes, primitive types, all from southern continents. A, from Africa; B, from South America; C, from Australia. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc., after Norman, Guide to Fish Gallery, British Museum.*)

Then the true (higher) mammals began to arise, also in the northern continents. They proved to be superior to the marsupials in the struggle for existence and drove the marsupials out—that is, forced them southward. Australia was then connected by land with Asia, so that it could receive the fugitives. South America may have been connected with North America or at least was so little separated that it was not isolated. These two continents were thus occupied by the monotremes and marsupials. Behind them the true mammals were coming; but before the latter reached Australia, that continent was separated from Asia, and the primitive types to the south were protected from further competition. Something similar happened in South America, but that continent's isolation was not complete; some of the mammals above the marsupials mingled with the primitive ones there. The situation in Africa is not so clear, but nothing is known that would forbid acceptance of the general theory.

Here again a peculiarity of distribution of world-wide extent has an
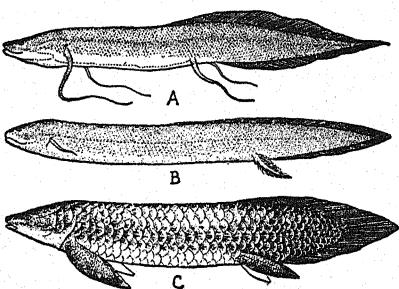
easy and reasonable explanation if types of animals have evolved as the earth evolved. No other origin of species would seem to offer any possibility of producing such distribution.

Island Life. If continents show a relation between geographic history and distribution of present forms of life, still more do islands reveal such influence. Islands generally are of two kinds, continental and oceanic. Continental islands are separated from a continent usually by relatively shallow sea, have gently sloping shores, and possess the same kinds of stratified rocks (limestone, sandstone, slate) as does the nearest continent. Obviously they were part of that continent and became islands by the sinking of the land. Oceanic islands, however, have steep sides, are separated from any continent by deep water, and are composed typically of igneous rock. They rose out of the bottom of the ocean by volcanic action and may or may not be capped with coral.

The British Isles are of the continental type. They have been separated from and connected with the continent of Europe across the North Sea or English Channel a number of times. The last separation occurred in what geologists call Recent time. The animals of these islands are mostly identical with those of the continent, even to species. The larger islands southeast of Asia (Borneo, Sumatra, Java) are also continental, but they were separated from that continent earlier, and their animals differ in somewhat greater degree from Asiatic ones.

Very different is the contrast between oceanic islands and even the nearest continents. In general they have no land mammals except bats which, like birds, are sometimes carried far by storms. Oceanic islands visited by man often have small rodents. Any fresh-water fishes they have are of the kinds that can adapt themselves to fresh water as they enter streams from the ocean. Animals that can be carried on floating material or borne by the wind, such as snails, lizards, insects, and land birds, are the types found on oceanic islands. A classical example is the Galápagos group, 600 miles west of South America on the equator —visited by Charles Darwin in 1835. Its land birds, reptiles, and insects are of species found nowhere else on the earth; yet they have a close resemblance to South American species. Among them are large lizards and tortoises which tend to be of different species on the different islands. The Cape Verde Islands have also their peculiar species, but these are similar to the African ones of the same groups. The Hawaiian Archipelago is farther from any continent than the Galápagos and Cape Verdes, and its species are more distinctive. Of Hawaiian plants, 83 per cent of the species are found only on these

islands; snakes are completely lacking; and species in general show less similarity to those of continents.

The relation of distance from continents to the similarity of faunas of islands and continents has an easy explanation if species have arisen by evolution. On any other theory of origins, these grades of likeness appear meaningless.

Continental Nuclei. The phenomena so far described are held to indicate, on a large scale, that species have evolved over long periods of time. Let us now examine more particularly some of the difficulties of the alternative supposition that species were created in precisely the form in which we now see them. The traditional concept of creation has been that it occurred at one place and all in a relatively short period of time, but perhaps we should ignore these features of the concept and assume that creation might be scattered all over the earth and all through the earth's history—subsequently, of course, to the origin of conditions suitable for life. Whether one extends the idea to include origin at many times and places will depend on what questions one seeks to answer.

A species created once and for all, with no changes in prospect, would be at the beginning not only anatomically in the form it has now, but would possess its present physiological properties including its often more or less automatic responses to features of the environment. A marine species would have been always marine—barring a few species which are able to enter streams and inland lakes—and a land species always terrestrial. The former would have been created in the ocean, the latter on land. From their—presumably single—place of origin they would have to go where they now exist if the present location is not the place of origin. A marine species would have had an open highway, inasmuch as all oceans are in communication with one another; but it would have been hampered by its reactions to different temperatures, to mechanical agitation of the water, to light (which penetrates in significant amounts only a thin surface layer of the oceans), and to the nature of the bottom materials. It would have been restricted also by the presence or absence of food organisms which likewise reacted in certain ways to all or some of the foregoing factors notwithstanding the connections between all oceans; therefore, marine species would not have been free to spread everywhere.

A land species would have been restricted much more, since land conditions are much more variable, land masses are not all connected, and very few terrestrial animals can readily cross arms of the sea. The geological evidence goes to show that continents and oceans have

long been roughly where they now are, though with many partial subsidences and emergences of the continents. In the midst of all the changes to which the land was subject, a number of land bodies have remained above water ever since the time at which, presumably, living things could first have existed. One of these continental nuclei was in Siberia and Mongolia, one in Canadian North America, one in Australia, one in South America, one in Africa, and smaller ones in Mexico and Central America, northwestern Europe, and elsewhere (Fig. 29). The precise locations are not important here; a land species originating early must have originated on one of them or have migrated
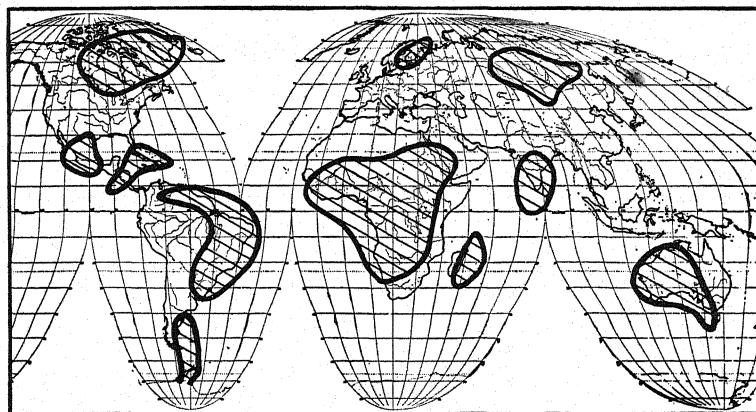
Fig. 29. Map of the world showing the continental nuclei. In each of the areas marked are lands that have never been under the ocean, although in most of them not all the land has been thus continuously dry.

to one of them when its place of origin became inundated. In either case it must have emigrated from its continental nucleus to any other terrestrial area which it now occupies. Its present location could hardly escape being determined in part by its place of origin. Let us see how well the present locations of species fit these suppositions.

Location of Species on the Earth. Species are limited to certain definite regions. Most of them are not even widespread, and almost none of them occupies a whole continent. The most striking examples of this restriction are found on islands more or less distant from other bodies of land. The distinctiveness of Hawaiian plant species has already been mentioned. Several thousand species of insects occur on these islands, and most of them are limited to this archipelago, while one whole family of birds including 60 species occurs only there. The

aye-aye occurs in Madagascar and is so different from any other species that it has been constituted a separate genus. Of some 260 species of birds in Madagascar, half are found nowhere else, many of them belong to genera peculiar to that island, and some even to families that are limited to it. Forty per cent of the species of plants and 96 per cent of the reptiles on the Galápagos Islands live only there. Forty-three species of birds are known only from Jamaica, 74 species only from the Bismarck Islands, one wingless bird (the kagu, allied to the bitterns and cranes) only from New Caledonia, one species of puffin only from the Cape Verdes. Fifteen species of Greenland plants are endemic, as are also about three-fourths of the 1000 species of plants in New Zealand. Not all islands are so distinct, for in Java only a few of the nearly 500 bird species are peculiar, and not a single genus is limited to it; but on the whole, the more isolated islands are characterized by many species not existing elsewhere. (See Fig. 30 for the location of some of these islands.)

The larger bodies of land also possess their peculiar species, but the areas are not so sharply marked off or so readily indicated. The yak is confined to the high mountains of Central Asia; South Africa alone has the secretary bird and two insectivores; only in tropical South America are there prehensile-tailed monkeys. While, as is more particularly pointed out later, species vary greatly in the amount of the earth's surface which they occupy, no species is found everywhere in the world, and most species are found only in a very small fraction of it. The important point here stressed is that, with very few exceptions, it is not the same fraction for any two species.

Almost as important is the fact that there are regions from which certain animals are excluded. When made concerning species, this statement is only a corollary of the preceding paragraphs. When it refers to larger taxonomic groups, it has added significance. There is no species of bear in Africa, for example. New Zealand and the Hawaiian Islands rival Ireland in their snakelessness. In the latter islands there are only seven species of reptiles of any kind; these are skinks and geckos. Java, which is not particularly individual in its fauna, in that it has most of the 176 species of mammals found in the Malay Archipelago, nevertheless does not contain elephants, tapirs, or bears. The Antilles, Madagascar, and the Malay Islands east of Borneo and Java lack cats. Oceanic islands in general are very poor in mammals, their principal representatives of this group being rodents and bats.

Meaning of Geographic Position of Species. How can these peculiarities of distribution have come about? The occurrence of a species
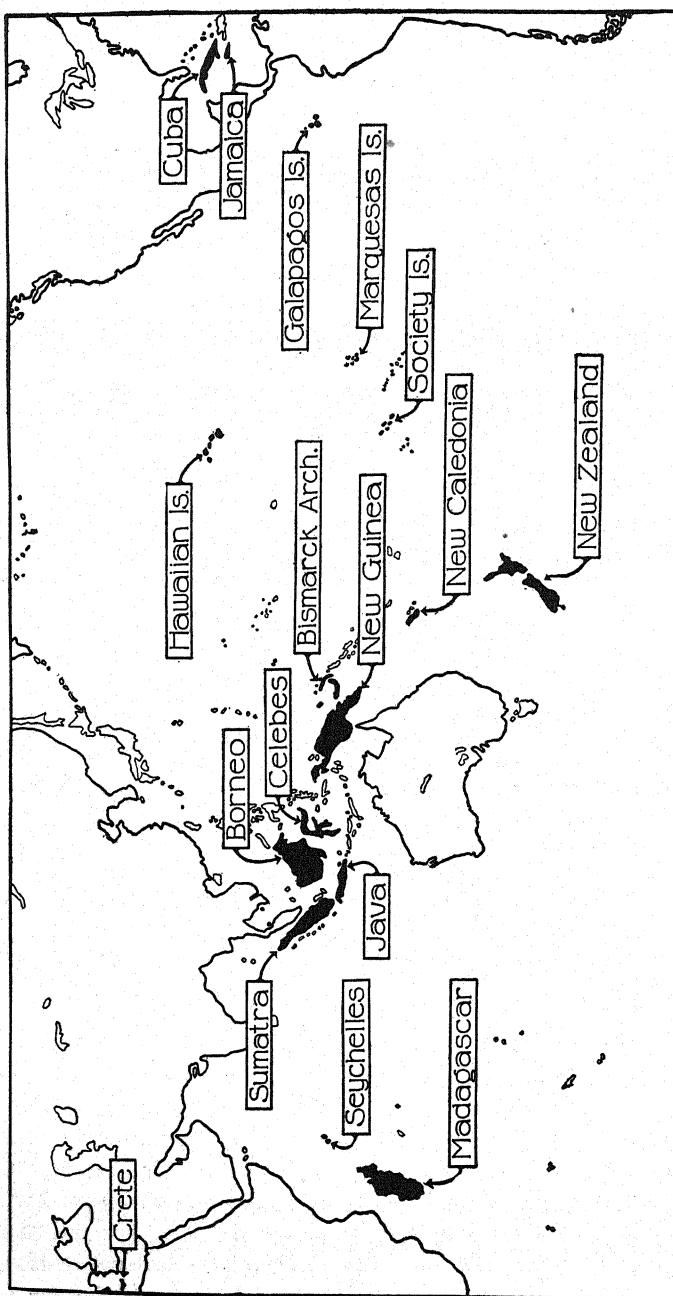
FIG. 30. Map showing the locations of some of the islands mentioned in the text.

only on a small group of islands might, if it were an isolated instance, conceivably be regarded as the result of extinction from the major portion of a once much larger range. But when many species are limited to a single small area, this explanation must almost certainly be rejected, since the original areas occupied by the several species must have been very unequal, and it is scarcely possible, purely as a matter of chance, that the extinction would have blotted out each of them from all regions except the small one which they now occupy in common. The Hawaiian group of islands may serve as an example. They are of volcanic or coral origin and have never been connected with one of the continents. If animals of all kinds arose in the form in which they now exist, it would fit the Hawaiian situation best to assume that land species, or at least some of them, originated on a Central American land nucleus. From this center they should have spread. It is a little peculiar, however, that they should have spread chiefly to the Hawaiian Islands, and still more peculiar that so few of them remained in Central America. While climate and other conditions may have changed so as to drive some species out of Central America, and while accidentally a few of these might have arrived at a hospitable situation only in Hawaii, it strains the laws of chance to have hundreds of species suffer the same fate.

Many Times and Places of Origin. To explain all the peculiarities of distribution, it seems necessary to assume that practically all habitable parts of the earth have witnessed the origin of species. The species of the Hawaiian Islands are most of them peculiar to that area because they originated there and have not been able to spread elsewhere. Those species which are common to the islands and the mainland could have originated in either or any of the places where they are now found and have been in some way transported to the other portions of their range. Snakes may be assumed to be absent because no snake species originated in Hawaii and none has been able to cross the water barriers. The species of birds and mammals now found only in Madagascar have probably never been anywhere else; they originated there and have not succeeded in passing beyond that island's confines. In like manner the peculiar New Zealand species may be supposed to have arisen in or near New Zealand, those of the Bismarck Islands, New Caledonia, and the Cape Verdes in or near their present ranges. With respect to species limited to portions of the continents it is not so clear that the species could not have migrated overland and be now considerable distances from their places of origin; and yet, it is questionable whether a species that had migrated far could be the same

species as formerly, though in raising this question one is taking for granted the evolution process which it is the purpose of this discussion to substantiate.

In general, it seems more reasonable to assume that, on the whole, species originated somewhere within, or not far distant from, their present ranges. This is a general statement and does not preclude the possibility that an occasional species has migrated widely and disappeared from its original haunts. Such an occurrence would generally depend upon a climatic or other change which rendered the original area unsuitable and would require presumably a long period of time. Allowing for even a considerable number of such migrations of all individuals far from the places of origin of their species, it must still be regarded as a highly probable generalization that species are now mostly around or near their starting points. Zoogeographers have often asserted that the present distribution of an animal type affords no clue to its point of origin. This statement is always made, however, of taxonomic groups of higher rank than the species. It is said that the fact that marsupials are almost limited to the Australian region and South America does not mean the marsupials originated in either of these continents. This is true, but the marsupials are an order. No student of distribution would maintain that any modern species of marsupial were among those in existence when first there were marsupials. All that is meant when it is said that marsupials are not now where they originally were is that the first mammals possessing the characteristics that mark off the marsupials from the other groups of mammals probably existed in one of the northern continents.

If species are at present not far from their places of origin, and species have sprung up all over the earth, it is clear that any nonevolutionary origin of kinds of living things must be somewhat different from the methods that have been proposed. But scattered origins of species are not only consistent with an evolutionary method of production; they are a necessary consequence of it.

Regional Similarities of Species. Were the peculiarities of distribution merely that each species has its own particular niche, to which it could not have traveled without occurring in various regions along the route of migration, it still would be possible to imagine that the origins of these species were all independent of one another. Whatever agency caused species to arise would only have had to operate in many places, be that agency evolution or anything else. There are many facts, however, which seem to require a relation of some sort between the origins of different species. General similarities among

species occupying neighboring areas imply such relations. The island of New Guinea has two genera of marsupials peculiar to it, but, as marsupials, they resemble the characteristic mammals of Australia and are correspondingly unlike anything in Asia. New Zealand likewise exhibits similarities to Australia, both in its animals and in its plants. The Bismarck Islands, in turn, have birds resembling those of their near neighbor New Guinea. The island of Celebes, the poorest in animals of any of the major units of the Malay Archipelago, has the babirusa, the black-crested baboon, and the dwarf buffalo, which are not only peculiar to the island but are closely similar to forms found only on three of the neighboring small islands. One family of plants including a hundred species on the Hawaiian Islands is also well developed in South America, but less so in other regions. On the Hawaiian Islands some 970 different kinds of snails (whether they be called species or subspecies, or merely phases is not very material) are found. To a large extent these forms occupy different valleys or groups of connecting valleys, and there is a gradual regional change among them. The species in any group of neighboring valleys are more like one another than they are like those of more distant valleys, and between two kinds distant from and unlike one another there is often a more or less steady change in the characters of the snails over the intervening valleys from one extreme to the other. It is generally true that two separated areas which have many species in common possess also species which, while not identical, are more closely similar to one another than any of them are to species in more distant areas. This is true of the Marquesas and the Society Islands, it is true of the Cape Verde Islands and the African mainland, and, at least with respect to plants, of Greenland and the North American continent.

It is not only the islands that show these similarities; the continents also have their faunal affinities. Australian animals are more like the South American, the North American animals more like those of Europe and Asia, than like those of other continents. The wapiti of the Rocky Mountains, unfortunately called an elk though not at all like the European mammal first called an elk, is very similar to the European stag, and still more like the Asiatic stag, the three forms being different species of the same genus (Cervus). The American moose, which is the sort of animal called elk in Europe, is so similar to the Scandinavian elk that they can almost be regarded as the same species. The caribou or reindeer of northern North America is very close to the Lapland reindeer. The American bison (Fig. 31) and European bison are two species of the same genus.

Just as significant are those differences between continents which are accompanied by great similarities within each continent. The monkeys of South America frequently have prehensile tails, but no Old World species has this character; the Old World species, except the manlike apes, have naked callosities on the buttocks not possessed by any American species. North and South America have many species of rodents, but the various species of ground squirrels, marmots, prairie dogs, beavers, meadow mice, jumping mice, and pocket gophers are all in the northern continent, while almost all the porcupines (six families, including 29 genera) are South American. All the sloths (two fam-
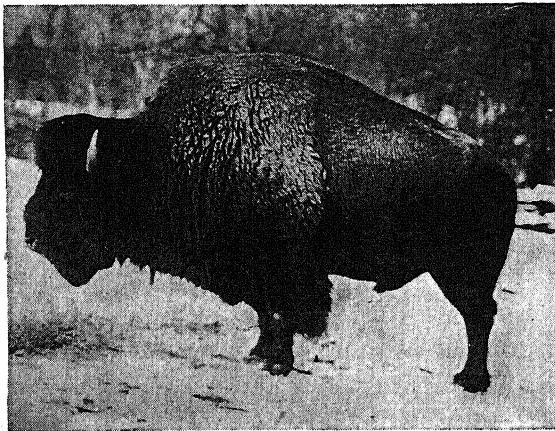
Fig. 31. American bison; another species of same genus is in Europe, nothing like it more distant. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc., photograph by National Zoological Park.*)

ilies), those curious slow-moving, long-limbed, hook-footed mammals which hang back downward from the branches of trees, are in tropical America. Two other families, the anteaters and armadillos, which are similar enough to sloths to be included in the same order, are likewise found only in tropical America, with the exception of one species, the nine-banded armadillo, which got as far north as Texas.

Congregation of closely similar species in limited parts of a single continent is very common. The several species of moles which are enough alike to be regarded as belonging to the genus Scapanus (Fig. 32) are all in the Pacific Coast states, while another group of species differing from the western forms so much as to be excluded from the genus Scapanus but similar enough among themselves to be another genus (Scalopus) is found scattered through eastern North America.

A number of species of chipmunks whose similarities are recognized by putting them all in the genus Eutamias are all in western North America, while members of the genus Tamias are all eastern. All zoogeography is marked by such examples. It is the rule that species much alike shall be near one another; any separation of species similar enough to belong to the same genus into two or more regions with wide gaps between, thus causing discontinuity of the genus range, occasions comment on its rarity and speculation upon the way in which it came about. The genera constituting a family show the same tendency to occupy the same general region of the earth, though the family ranges are larger and discontinuity is not so rare.
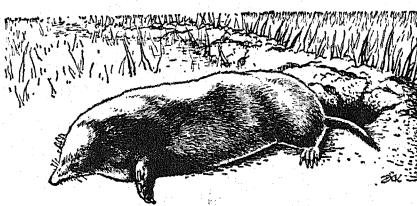
FIG. 32. Mole of genus Scapanus which is limited to Pacific Coast area. The genus Scalopus is entirely eastern. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc.*)

Sometimes the similarities are not what would be expected on geographic grounds, for the fauna of Madagascar is most similar, not to that of its near continental neighbor Africa, but to that of Asia, the gap being bridged over by the Seychelles Islands whose animals are similar to those of Madagascar. The animals of New Guinea, as pointed out above, are similar in general to those of Australia, but quite different from those of almost equally near islands to the north and west; and the fauna of Sumatra is more like that of Borneo than like that of its nearer neighbor Java. These peculiarities all have their special explanations, which it is beyond the province of the present chapter to discuss; the phenomenon to be emphasized is that regions geographically near one another usually show greater similarities of their living forms than exist between more distant areas.

Were species entirely independent of one another in their origins, such regional similarities could hardly exist. There must be some relation, genetic or otherwise, between species so located. The genetic relation is the only one that has ever appeared to be a satisfactory explanation. Origin of species by evolution from other species is not only in agreement with such geographic collections of similar species; it would almost necessitate their existence. A group of species derived, in a given part of the world, from a common stock, from which each came to differ, at the time of its origin, in a few minor respects, could

not well avoid showing among themselves greater similarities than any existing between them and species developed from an unrelated stock.

Is Age of Species Indicated by Spread? Among the numerous species which are limited to one well-defined portion of the earth are not a few whose areas are remarkably small. These diminutive ranges are especially impressive when they are compared with others which extend over most of a continent, or into two or more continents. Taking the earthworms of Canada and northern United States, which are of the same species as those of Europe, as a not extreme example of the great size to which a range may extend, let us examine some of the smaller areas. One species of violet is known from only a few square yards in the Hawaiian Islands. Several species of trees peculiar to this archipelago are found only on a 56-acre tract surrounded by lava. One of these species was at first described from only a single specimen, but more are now known. The lava strongly suggests that the range was once somewhat larger, but it can never have been very extensive. A flightless cormorant is found only on Albemarle Island of the Galápagos group. The smallness of these island ranges is not usually difficult to explain, especially where a whole island is occupied, since the sea is an effective barrier against migration of many species. For such species, if their origin within their present ranges be accepted, smallness of area must usually follow. It is otherwise, however, on the continents. There is a species of lizard which is found only in the southern peninsula of Greece, with perhaps some representation on the island of Crete. Another species of the same genus (Lacerta) occurs in its typical form all through central Europe and the Mediterranean states, while if its subspecies be included the species extends into western Asia and northern Africa. A species of toad is found only in Texas, while another species of the same genus (Scaphiopus) occurs in most of the states from the western plains to the Pacific Coast. A species of turtle is limited to southwestern Texas and the adjoining portion of Mexico, while another species of its genus (Gopherus) ranges through almost the whole of the southern states. A species of tree frog is concentrated in southeastern New Jersey, with scattering representation in the coastal regions of the Carolinas; another species of the same genus, *Hyla versicolor* (Fig. 33), has spread over the eastern half of North America.

The differences between the sizes of ranges in the last several examples can hardly be explained by barriers. Probably none of these species has reached insurmountable obstacles to its migration on all sides. One of the turtles mentioned as occupying a small range is

a desert species, but apparently has not occupied all the desert areas directly open to it. So far as can be ascertained there is nothing peculiar about the small New Jersey area occupied by one species of Hyla that would account for the absence of that species from the regions around it. Such statements have to be made with caution, for
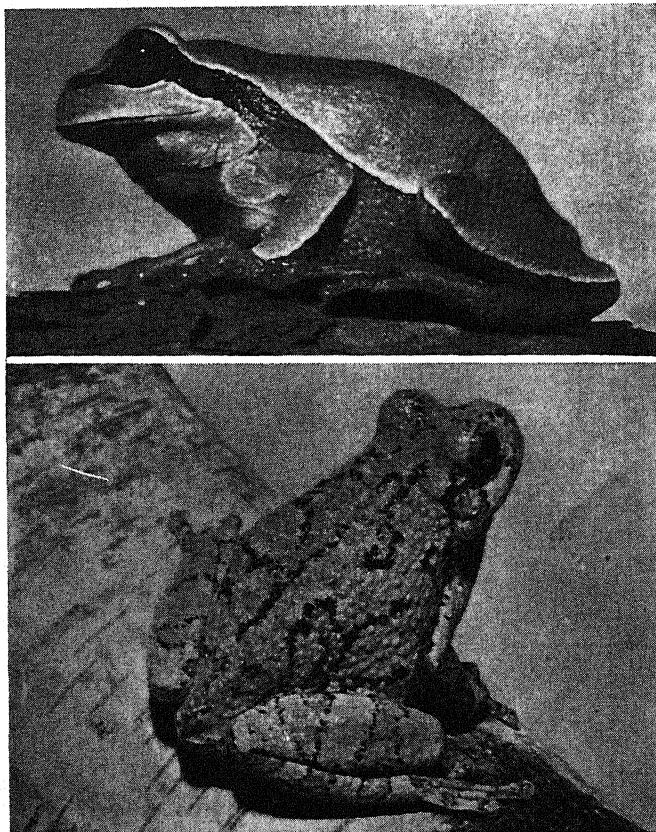
FIG. 33. *Hyla andersonii, above*, whose range is concentrated in southeastern New Jersey with scattering representation in coastal areas to the south, compared with the range of *H. versicolor, below*, which extends from Canada to the Gulf states east of a line from Montana to Texas. (*Courtesy of Isabelle deP. Hunt.*)

the physiological properties of animals are never fully known, and there may be undiscovered features of their environments that could act as barriers. Yet the safest way to use evidence is to accept it at face value after the most careful study and then attempt to discover what it means. The evidence is that some species have smaller ranges

than others that are very similar to them, when there is nothing either in the animals themselves or in the environment which would appear effective in preventing the enlargement of the small ranges.

The principal other conceivable reasons for smallness of range are (1) that the species is young and has not had time to spread far, (2) that its powers of multiplication or migration or both are limited, and (3) that it is approaching extinction, being perhaps very ancient. The last possibility should be relatively uncommon, because extinction is apt to come about rather suddenly after a species has got down to small numbers of individuals. Approaching extinction is apt to be recognizable, also, by the absence of any very similar species near it. For example, a lizard species of the genus Cricosaura, which is held to be archaic, is found only on a few hundred acres of coastal plain near Cabo Cruz, Cuba. No similar lizard species is anywhere near. Restriction of range due to the youth of a species and that due to low fertility or sluggish migration are not easy to distinguish. Seldom is enough known about the properties of a species to say which of these two is the governing factor. In one genus of plants it is possible to eliminate age as the principal factor of spread, namely shepherd's-purse (genus Capsella, Fig. 34). From certain facts regarding

FIG. 34. Shepherd's-purse, *Capsella orientale* Shull, a wide-ranging derived species. (*Courtesy of Professor George H. Shull.*)

chromosome number, to be explained in a later chapter, supported by the known mode of inheritance of shape of seed capsule in one species, is is practically assured that certain species are derived by a simple step from certain other species. In general, the derived species, which would be younger than those which gave rise to them, have the larger ranges. This is true in various parts of the world. The derived species in general are simply more successful than their parent species.

Among the Hylas referred to above, it seems to be the opinion of herpetologists that the New Jersey species is young though it is impossible to be sure.

The idea that size of range depends on the age of the species, that is, on the duration of its process of spread, was emphasized by Willis under the name "age and area hypothesis" in 1922, but it is more than a century old. Considerable support for the theory is found in the distribution of many different types of living things. Unfortunately, however, for the use of this support here, it relates largely to taxonomic groups higher than species. It has been the purpose in the foregoing discussion to employ only species for contrast, since the use of genera or families or orders would necessarily involve to some extent the view that higher ranking groups had evolved from lower and would savor of arguing in a circle. The evidence that would most conclusively show area to be dependent on age would be to find deeper, hence older, fossils of some wide-ranging species, and only shallower fossils of some closely circumscribed species. Paleontologists are not blessed, however, with abundance of fossils belonging to living species. Only a few fossil forms very closely resemble modern animals or plants, and it is very unlikely that even in these few cases the fossil type could be regarded as of the same species as the modern, if its anatomy were sufficiently preserved to make an adequate comparison possible. When larger groups are used, there is some evidence that those having the deeper fossil representatives are on the whole the more widespread; but these comparisons to be valid must rest on the assumption that all members of the group are genetically related to each other, which is an evolutionary assumption.

Time of Origin of Species. Whether size of range furnishes valid evidence of the age of a species is not, however, a crucial matter. There are other indications, the general nature of which has been pointed out in this chapter, that some species are old and others young. The implications are that at every period of the history of life since its early stages there have been young and old species. That is, species have been arising at frequent intervals throughout that time. This situation fits an evolutionary origin admirably. If species came into existence by modification of some individuals of an older species, these groups would necessarily be of unequal ages. The whole evolutionary scheme would require the development of new species, one after another, on a magnificent scale.

If, to match these facts, creation be regarded as occurring anywhere on the earth and throughout the time in which life has existed, the

creational concept may be rescued. But it still must leap a hurdle not yet mentioned. When a new species is created, the creation must occur at or near the place where a species very similar to what the new one is going to be already exists. The creation can hardly be called an *independent* origin. If, however, creation is to be endowed with most or all of the attributes of evolution, the debate concerns only the meanings of words.

FOSSILS EXPLAINED BY EVOLUTION

Thus, on the theory of descent with modification, the main facts with respect to the mutual affinities of the extinct forms of life to each other and to living forms, seem to me to be explained in a satisfactory manner. And they are wholly inexplicable on any other view.

—CHARLES DARWIN, 1859

When the structure of the earth and the building and rebuilding of its crust are understood, it is easy to show that the organisms of one period of time were very different from those of earlier or later periods. That is demonstrated by the fossils, which are representative of the animals and plants of those times. If it could be assumed that early beings represented by fossils were ancestral to those which produced the later fossils, the fact of past evolution would need no other proof. The assumption of such genetic connection is more reasonable than any other hypothesis that might supplant it, so one would suppose that the facts of paleontology must early have suggested to naturalists that evolution on a large scale had occurred. Actually, however, knowledge of fossils was not one of the prime stimulants of evolutionary ideas. Lamarck, the earliest avowed evolutionist of any great significance, arrived at his concept of evolution largely on other grounds. Though he studied fossils and used them to support his evolutionary views, that development came late in his life and was a consequence rather than a cause of his advocacy of evolution. Darwin, a later most important contributor, leaned heavily on other considerations. While in his "Origin of Species" fossils are employed, his discussion of them is introduced by a chapter entitled "On the Imperfection of the Geological Record," which seems to indicate that he felt the contradictions offered by fossils to his theory more keenly than he felt their support. This discussion is preceded by chapters on artificial selection, the effects of domestication, classification, population increase, instinct,

the physiology of variation and hybridization, indicating presumably a greater reliance placed on these as evidence or as material influences. Finally, Cuvier, who was among the great students of fossils at the time when the evolution doctrine was being seriously advanced, saw fit to oppose that explanation vigorously.

There were reasons for this backwardness of paleontology as a stimulant to early evolutionary thought. Knowledge of fossils in the early nineteeth century was very meager compared with that of the present time. Moreover, geology was itself then only struggling toward a rational interpretation of earth features. The uniformitarian doctrine, according to which geological processes have been of the same general sort through long periods of the earth's development, and which has been one of the major unifying factors in geology, was first proposed and generally rejected in the eighteenth century and required the great weight of Sir Charles Lyell's authority to establish it well along in the nineteenth century. Lyell at first adhered to the view that species are permanent, and later when he adopted the evolution concept it was under the influence of Darwin's studies, with which he was acquainted long before their publication in the "Origin of Species."

At the present time fossils constitute one of the most convincing indications of the origin of species at different periods and of the general course which evolution has taken if the assumption be made that all forms, or at least large groups of them, are genetically connected with one another. Contrary assumptions have sometimes been made but appear to be untenable, for reasons to be stated later. It is the purpose of this chapter to show the unlikeness of organisms of different periods and to develop the reason for regarding them as genetically connected.

Geological Periods. In order to refer intelligibly and briefly to events in geological time, it is most convenient to employ the names of periods which are naturally marked off from one another by events that plainly occurred in the development of the earth. When stratified rocks, which must have been deposited under water, are sheared off obliquely and are covered by totally different stratified material set at a different angle, it is apparent that the construction of this portion of the earth took place during two periods of submergence, separated by a period of elevation above water accompanied by erosion. When the masses of dissimilar stratified rock contain strikingly different fossil forms, it appears certain that a considerable time elapsed between the submergences. On the assumption that extinct forms lived in situations similar to those in which the modern organisms most like them

Fossils are unknown in these formations. The occurrence of graphite in them is, however, taken to mean that simple plants capable of carrying on the carbon cycle then existed. Enormous masses of limestone of the same age also probably owe their origin to secretion by plants; for, though limestone may be deposited by chemical action, deposits known to be formed in this way are of local occurrence and are derived from earlier limestone. In the Proterozoic there are unquestionable fossil animals and plants. Almost all the plants are algae, some of the colonies of these found in limestone being a foot in diameter. Among animals, siliceous sponges of that age are exposed in the Grand Canyon, and burrows believed to be those of worms have been found in Proterozoic sandstone in Montana. Glacial till in Canada in the Huronian formation, and in the Australian region in somewhat later deposits, indicate cold climate at least twice during the Proterozoic.

The Cambrian Outburst. Compared with the paucity of fossils in the Proterozoic deposits, the Cambrian has the appearance of pouring out a deluge of living things in great variety. As if suddenly, all the principal phyla of animals are represented in deposits of this period. Geological periods are all inconceivably long, and Cambrian was probably one of the longer ones; but even after making allowance for this great span of time, the occurrence in it, for the first time, of many hundreds of species so diverse as to belong collectively to most of the phyla that have ever existed is an apparently abrupt beginning. The abundance and variety of life are rendered even more impressive by the consideration that almost certainly only a small proportion of the existent types were fossilized. That Cambrian life was not the sudden eruption which it appears to be is, of course, the view of biologists in general, for it is regarded as the result of a long period of unrecorded evolution. Since in the main only organisms with hard parts are abundantly preserved, and since by an evolutionary origin the earliest living things can hardly have possessed such hard parts, the assumption of a long period during which living things existed without fossilization is a reasonable one. No emphasis is here placed, however, on the probability of an abundance of organisms in Proterozoic and earlier periods. For the purpose of this chapter is not to explain the discrepancies of geological history, by making evolutionary assumptions; it is rather to discover to what evolutionary conclusions one is driven by consideration of the patent facts regarding fossils. Viewed in this light, Cambrian does present the outburst of life that is so apparent. It is from that period that the paleontological story of evolution must start. Let us see what the beginning was.

The most abundant of all fossil forms in the Cambrian were the trilobites, which belong to the Crustacea, and were more nearly like modern fairy shrimps than any other living group. They have long been extinct. The body was flattened and marked by longitudinal grooves into three lobes (Fig. 36), hence the name. The trilobites increased throughout Cambrian time, both in numbers of individuals and numbers of species; over a thousand species have been described from that period. Next in abundance were the brachiopods. These animals superficially resemble clams, because they possess a shell of two hinged valves (Fig. 37). They were long classified with the mollusks, until it was appreciated that their internal structure was not at all that of
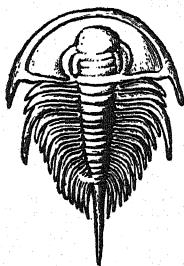
FIG. 36. A trilobite.   FIG. 37. A brachiopod.

(*Both figures from Pirsson and Schuchert, Textbook of Geology, John Wiley & Sons, Inc. By permission.*)

mollusks, and that the two valves, instead of being right and left as in clams, were dorsal and ventral. The Cambrian brachiopods possessed shells mainly of a horny substance. Hundreds of species are known from Cambrian marine deposits.

Mollusks were less abundant than either of the foregoing groups but were represented by each of the principal classes—the clams, the snails (mostly not spiral), the pteropods, and the cephalopods. Of the echinoderms, there were a few starfishes and a few sea cucumbers, and a somewhat larger number of the primitive and extinct group known as cystoids. The worms, soft-bodied as they are, were not often preserved as fossils. A notable exception is the Burgess shale, an exceedingly fine-grained deposit in British Columbia, in which a great variety of impressions of worm bodies are preserved. Elsewhere their presence in the Cambrian is abundantly indicated by their tracks and burrows in the mud. Jellyfishes are even less likely to be fossilized than are the worms; yet in many places in both America and Europe are

found casts of the interior cavities of their bodies. Other coelenterates, including corals and the extinct hydroidlike graptolites, the former abundant enough to constitute reefs, have been assigned to the Cambrian, though there is some doubt regarding both the affinity of the organisms and the identification of the containing rocks. The sponges, as might be surmised, are identifiable only by the needlelike spicules of their skeletons, but these are fairly common. Protozoa, the one-celled animals, were represented by both Foraminifera and Radiolaria.

The animals mentioned above belong to at least eight of the main groups or phyla. The worms probably all belonged to the Annelida, though it is possible that one of the other wormlike phyla was included. Assuming, however, that the other worms are not included, there remain only two other phyla of minor importance, and one major phylum, chiefly the vertebrate animals, unaccounted for. Since all these omitted groups with the exception of the vertebrates were soft-bodied, they may easily have existed in Cambrian time. Even the vertebrates may not have been absent, since fishes appear in the very next period, and an object that looks like one of their scales has been found in Cambrian rocks. It is thus clear that in Cambrian time most of the great groups of animals were already in existence.

Of plants, only fossil seaweeds have been found. Abundant plant life in the sea may be inferred on the ground that the animals must have been ultimately dependent, as they are now, upon plants for food.

The further history of life on the earth can best be told in relation to the several groups of organisms, rather than to the geological periods.

The Arthropods. The trilobites, with which the arthropods began so auspiciously in the Cambrian, waxed more abundant in the Ordovician, but reached their peak in that period with 1200 known species belonging to 125 genera. Only a few of these genera, however, are the same as those of the preceding Cambrian. Of the 13 families to which these 125 genera belonged, only 3 survived from the Cambrian; the rest were new. No new family arose after the Ordovician period, though new genera continued to appear. Only about half as many species of trilobites have been found in Silurian deposits as in Ordovician, and none of these is a survivor from the Cambrian. The group was obviously declining; only about 200 species occurred in the Devonian. New species and new genera appeared during this decline, but larger numbers of both species and genera became extinct. The decline was accompanied by curious ornamentation of the head and the development of remarkable spines on the head and tail in the new

species that arose. Trilobites were rare in the Carboniferous period, and none whatever later than Permian is known.

The eurypterids, resembling scorpions but living in the sea instead of on land, appeared first in Upper Cambrian, were still unimportant in Ordovician, increased in numbers and size in Silurian, and reached their maximum in both size (10-foot specimens being found) and variety in Devonian. Thereafter they declined, and the last ones known came from Permian deposits.

The horseshoe crabs, which first occur in the Silurian of Europe, never attained great variety or abundance, but they have survived to the present time. During the earlier geological periods, different genera arose successively, but by Jurassic time only the genus Limulus existed, and this genus survives today on the east coast of the United States and in the Moluccas Islands. Probably only so old a genus could now occupy two such widely separated areas.

While a primitive wingless type of insect is known from Devonian, that group does not appear again until the Pennsylvanian division of the Carboniferous. The abundance and large size of insects then—2-foot dragonflies, 4-inch cockroaches—suggests they had been developing a long time. Never since Pennsylvanian and early Permian have insects been so large, and it is suggested that the decline in size was correlated with the onset of colder climates. In Permian time the dragonflies and May flies were the most conspicuous. Late in that period appeared the first beetles, in Australia. In Triassic, for some unkown reason, insects were scarce, only about thirty species of all kinds being known; but they blossomed forth again in the Jurassic with multitudes of individuals and such new types as grasshoppers, bees, wasps, ants, flies, and butterflies. Almost all insects of Jurassic time were smaller than in the preceding ages and were of quite modern type. No very important change in them is revealed during the Cenozoic era, though fossil insects of that time are not very numerous. Insects are today more abundant in species than any other group and more abundant in individuals than most others.

While arthropods of other kinds have been found, they were not very favorable for fossilization, and connected accounts of their changes are not so readily available.

The Brachiopods. At their beginning in the Lower Cambrian, the brachiopods were mostly of a group having horny and phosphate shells, but later in that same period they were chiefly of calcareous type. The latter became increasingly prevalent in later periods. Brachiopods increased greatly in Ordovician, over 3000 species being found

in this period and the Silurian together. Great beds of limestone were produced by them. Two of the families gained at the expense of all others as the group went over into the Devonian, and in this period the group attained its greatest abundance and diversity. During the Carboniferous period brachiopods maintained their individual abundance, but a decline set in in the number of species and genera. New kinds were coming into existence, but they were more than offset by the loss of older forms. This decline continued, though slowly, so that throughout Paleozoic time brachiopods were so abundant that they are extensively used by paleontologists as index fossils. Being of different species and genera in successive ages, and being of well-nigh world-wide distribution, they have been used to correlate deposits in widely separated areas. Their value for this purpose was greatly diminished in Mesozoic time because, while they were fairly abundant in Europe, only a few genera were left by Jurassic time, and North America, for some unknown reason, was poor in them. Through the Cenozoic era they were inconspicuous, but about 225 species have survived to the present.

The decline of the brachiopods is notable for the tenacity with which certain genera maintained themselves. The very considerable diminution in number of species and genera which began in the Carboniferous involved the destruction of most of the genera of Devonian time; yet among the survivors were several genera that first appeared as early as Silurian. Even more striking examples are the genera Lingula and Crania, which were among the earliest of the Cambrian forms and were of the horny-shelled type that was largely displaced by the calcareous type before the end of Cambrian, but which are still in existence, living, at the present time. These brachiopods thus exhibit even greater permanence (stability, it would be called, with the evolution concept in mind) than the Limulus mentioned earlier among the arthropods. No satisfactory explanation of the persistence of a few genera, when nearly all genera are much more short-lived, has ever been offered.

Bivalves and Snails. As we have seen, the mollusks were already divided into their main classes when they were first preserved in the Cambrian. All these classes increased greatly in the Ordovician. For the clams, this increase was largely one of numbers; for the snails it was a change in numbers and kinds, and in size, particularly among the spiral-shelled forms. In both of these classes there was moderate further increase in variety through the remainder of the Paleozoic, and their numbers were well maintained. Clams and snails are not,

however, particularly good index fossils for the Paleozoic era, because their distribution was at times limited. In some situations they were abundant, elsewhere lacking. This may be in part due to the rather ready solubility of the mother-of-pearl which lines their shells. This layer was relatively thick in the early mollusks. The outer material, which is less soluble, was relatively thicker in the later forms, and this feature may have helped to preserve them. At any rate, in the Mesozoic both clams and snails were much better represented, and were far more varied, than in the preceding era. Oysters (bivalves) first became abundant enough to form banks in the sea in Jurassic, such banks being duplicated in the Cretaceous. By the end of the
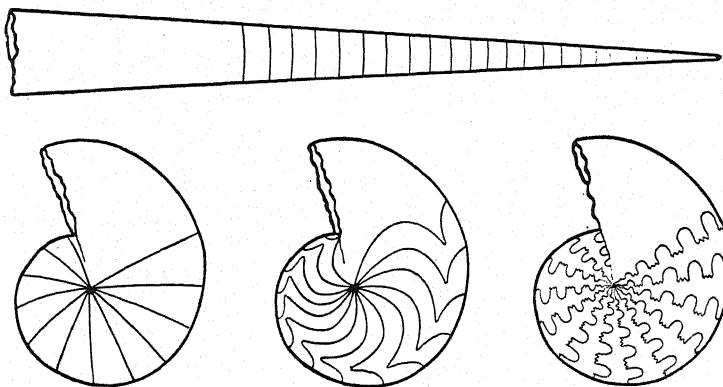
Fig. 38. Fossil cephalopods. *Above,* orthocone; *below, left to right,* nautiloid, goniatite, and ceratite.

latter period, bivalves were largely of modern type, many of the genera then existing being still living at present. Snails reached their general modern composition by the end of Cretaceous, owing to the appearance then of genera which have persisted throughout Tertiary time to the present. Although oysters attained in the Miocene a size which they possessed neither before nor after that time (fossils from California measuring 13 by 8 by 6 inches), these two groups of mollusks cannot be said to have culminated in any past period; for, with their more than 40,000 species, they are as abundant and as diverse now as they ever have been.

The Cephalopods, an Evolutionary Tree. Because of their different history and their special significance in evolution discussions, the cephalopods are separated here from the other mollusks. Reference is made only to the four-gilled types, of which the modern Nautilus is one, not to the squids and cuttlefish, whose history is not so instructive.

The early forerunners of our nautiloids had straight conical shells. At any moment of its life, the animal occupied chiefly a short segment at the wide end of its shell. Behind it was a partition which it had recently secreted. Behind that partition, toward the tip of the cone, were other partitions, each representing a former posterior limit of the animal when it was younger. As the body grew, additions to the shell were made at the wide (open) end, and periodically the animal slipped forward and secreted a new partition behind it. The partitions
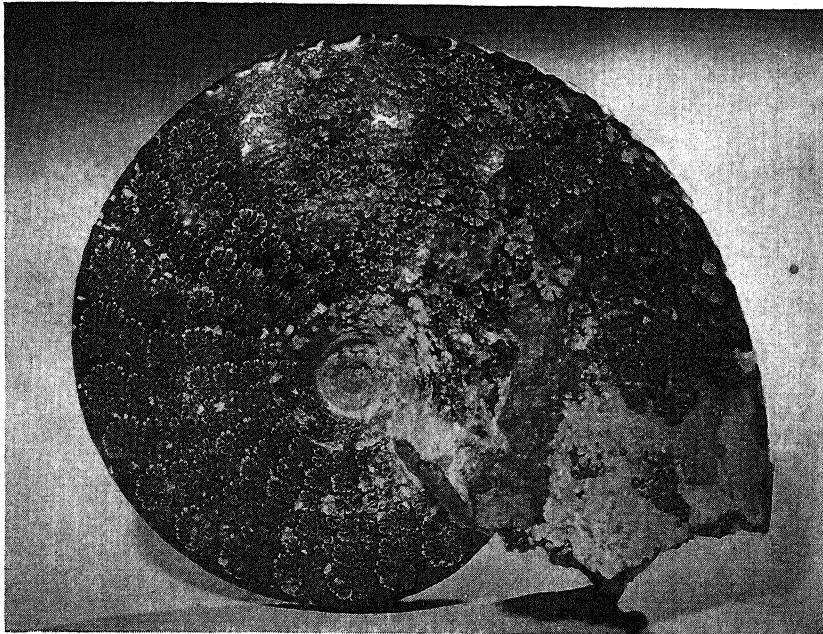
FIG. 39. Fossil ammonite. (*Ward's Natural Science Establishment.*)

cannot be seen if a whole shell is present, but in fossils the outer part is frequently removed so that the sutures (edges of the partitions) are conspicuous. These orthocones, as they are called, may have begun in Cambrian and were common in Ordovician. One genus ranged in size up to 10 or 15 feet (Fig. 38). This large orthocone persisted into the Mesozoic, though the group as a whole declined.

In the Silurian the characteristic cephalopods had coiled shells. In their internal structure they were not very different from the orthocones, though the sutures were moderately curved. This is the type that resembles our modern living Nautilus, and its members are ac-

cordingly called nautiloids. Then in the following period (Devonian) the sutures were characterized by a few rather sharp angles, with saddlelike curves between. The partitions were no longer the simple saucers they had been. Cephalopods of this form are known as goniatites (Fig. 38), from a common genus name.

Further complications of the sutures appeared in the Carboniferous, when the sutures were thrown into numerous U-shaped curves which showed, at characteristic points, a zigzag or saw-toothed form. These cephalopods are called ceratites, again from the name of a common genus. Finally, beginning in the Permian but increasing in the Triassic, the sutures were transformed into the remarkable lobed and foliaceous
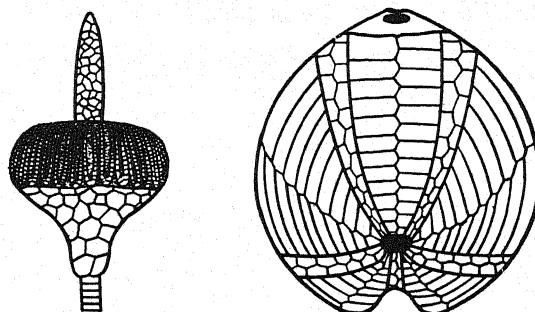
Fig. 40. Fossil echinoderms. *Left,* crinoid of early Carboniferous; *right,* sea urchin with 20 rows of plates and bilateral symmetry, from Cretaceous.

patterns of Fig. 39. These forms are the ammonites. They continued through the remainder of the Mesozoic but died out in the Cretaceous.

The chronology of the four-gilled cephalopods is not quite so simple as the foregoing account might seem to imply. The orthocones lasted into the Triassic, long after nautiloids and goniatites arose. The nautiloids persist alive today—the only type that has done so—but are limited to not more than four species at the bottom of the eastern Pacific and the Indian Ocean. Both goniatites and ceratites overlapped, in time, the ammonite group. Yet there was a succession, most readily noted in the first occurrence of the several types, and in general also in their periods of greatest development. Such a series of forms, differing by only moderate steps from those which immediately precede or follow, is what is called a line, or better, a tree, of evolution, even though no genetic connection can be definitely proved. The significance of such trees is pointed out toward the end of this chapter.

The Echinoderms. Most of the Cambrian members of this phylum were of the now extinct class of cystoids, though there were some

starfishes and sea cucumbers. Of this whole phylum, only the crinoids and sea urchins appear abundantly enough to furnish a real history of their changes. The crinoids were present but not common in Ordovician, increased in numbers and variety through the succeeding periods, and reached their maximum (about 600 known species in North America) in the early Carboniferous (Fig. 40, left). They were reduced in numbers but began to be radically changed in structure to conform to the modern type in Jurassic, after which the new type became in turn abundant. Free-swimming species first appeared in Jurassic and were locally abundant. Since that time they have been relatively unimportant. The sea urchins, which appeared rarely in
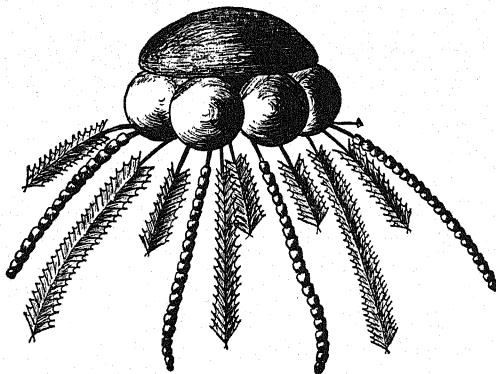
Fig. 41. Fossil graptolite from Ordovician. (*From Hussey, Historical Geology, McGraw-Hill Book Company, Inc.*)

Ordovician, did not become abundant until Jurassic and Cretaceous. They are today the commonest of echinoderms. Two striking changes in their structure are demonstrated by the fossils. First, modern sea urchins have 20 rows of plates in their tests, or shells, while all Paleozoic members of the group have either more or fewer rows. Second, forms showing right- and left-sidedness appeared first in Jurassic; all earlier species had been radial. Figure 40, right, shows both of these features in a Cretaceous fossil.

Other Invertebrates. Of the remaining invertebrate phyla, the ones most commonly met with in marine deposits are the coelenterates, sponges, and protozoa. In the Burgess shale, where some of the most remarkable preservations of ancient life occur, there are unmistakable impressions of jellyfishes. The graptolites (Fig. 41) reached their maximum in the Ordovician, in forms arranged in rows on both sides of

the stem. By Silurian time they were much reduced and were mostly those forms with only one row of individuals; and before the end of the Devonian they were extinct. Corals of both the hydroid and the true (anthozoan) type were present in Ordovician, the former abundant enough to produce reefs. The true corals of this time possessed partitions in multiples of four, as contrasted with six in modern corals, a type which did not make its appearance until the Permian. Both hydroid and anthozoan corals expanded rapidly, in species rather than in genera, from Ordovician to Devonian, but suffered reverses in the Carboniferous and Permian, since reefs were reduced in the former,
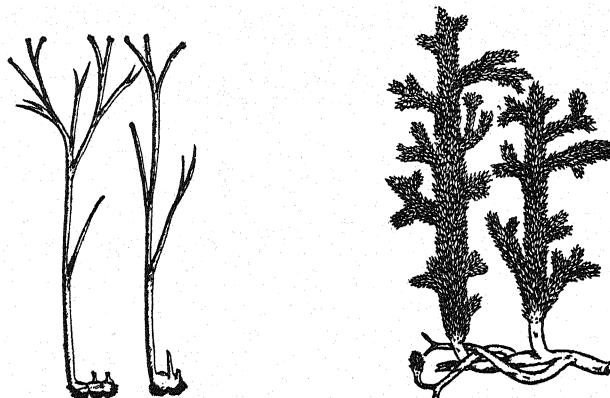
FIG. 42. Devonian land plants. (*From Hussey, Historical Geology, McGraw-Hill Book Company, Inc.*)

and wanting in the latter, of these periods. In later periods they regained their abundance, but the true corals were then of the basic six-partition type as are the reef builders of the present.

Sponges are preserved only with respect to their skeletons of spicules, and these show characteristic changes of form. The protozoa are represented only by shelled forms, mostly Foraminifera and Radiolaria, which constituted so small a part of the probable protozoan life of any period as to make the history of their changes unimportant for our present purpose.

Land Plants. It is not to be expected that plants would be well preserved until they possessed woody structures. The early Devonian land plants were mostly devoid of leaves, or their leaves were mere scales (Fig. 42). One important group of that period, the pteridosperms, was long regarded as belonging to the ferns, but it is now known that they bore seeds, as modern ferns do not. Stems of some of these were

3 feet in diameter. The lycopods, or club mosses, whose modern examples are such small plants as the ground "pine" and the creeping Selaginella, were then trees, up to 30 feet in height. Trees resembling the pines, firs, and spruces also existed then, but they did not possess needlelike leaves.

The giant treelike club mosses (Fig. 43, left) were very abundant in the Carboniferous and grew in all the northern continents; but by Permian time they were rare and were missing from the Triassic. The horsetails of the upper Carboniferous were trees with transverse
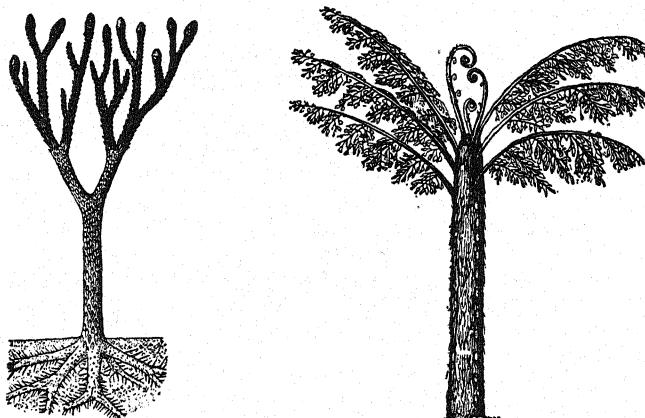
Fig. 43. Giant club moss (*left*) and tree fern from upper Carboniferous. (*From Pirsson and Schuchert, Textbook of Geology, John Wiley & Sons, Inc. By permission.*)

joints, some with branches, some without. They were still abundant and large, though largely of different genera in Triassic and Jurassic. Since then they have gradually taken on the characteristics of the modern members of the group, the scouring rushes, which are reduced to one genus and some twenty-five species, very few of which grow over several feet in height.

The pteridosperms, referred to above in the Devonian as having been regarded as ferns until they were found to be seed bearers, reached their maximum development in the late Carboniferous. They were still abundant in Permian, much less so in Triassic, and after that disappeared. The ferns (Fig. 43, right) were common, however, all through late Paleozoic, uncommon in Triassic, but abundant again from Jurassic to Eocene. After that they were mostly replaced by modern plants.

The Devonian "conifers" had straplike leaves, rather than needle-

shaped. The same kinds of leaves are found on those of the Carboniferous (Fig. 44). They are classed with the conifers, though their seeds, instead of being borne in cones, were situated on small budlike branches. Cones first appeared in late Carboniferous and early Permian, on a tree that had narrow leaves. The splendid petrified trees of the far southwestern states were conifers of Triassic time; some of them show annual growth rings, indicating seasonal differences of climate, though perhaps not temperature extremes.

A few true cycads occur in early Triassic, many more in late Triassic, mainly represented by their leaves. In Jurassic they became so abundant that this period is often known as the "age of cycads." In late Cretaceous, however, they were largely overwhelmed by the flowering plants, and today they constitute an unimportant group of which the sago "palm" is the most familiar example. Somewhat similar to the cycads are the ginkgoes. Appearing first in Permian time, they became abundant in Triassic and especially Jurassic. With the coming of the flowering plants in Upper Cretaceous, the ginkgoes too receded in importance, and the group is today represented by only one species, widely cultivated as an ornamental plant and probably nowhere wild.

Fig. 44. Large-leaved late Carboniferous evergreen, Cordaites. (*From Pirsson and Schuchert, Textbook of Geology, John Wiley & Sons, Inc. By permission.*)

The true flowering plants appeared suddenly in such abundance and variety in late Cretaceous that it is generally assumed they originated much earlier, though little fossil evidence of them in earlier periods has been obtained. They must have migrated into the places where they are found, from other regions in which they either were not preserved or which have not been explored, possibly from arctic areas. It is the woody or otherwise hard plants that are preserved, and the late Cretaceous forests include oaks, beeches, maples, elms, poplars, magnolias, tulip trees, and palms, and grasses are also abundant in the open places. The forests were thus much like those of the present.

Fishes. The earliest certainly known vertebrates are Ordovician fishes of the group known as Ostracoderms, found in Colorado, Wyo-

ming, and South Dakota. These armored fishes (Fig. 45), mostly of small size, reached their maximum abundance in Devonian and perished in that period. The lampreys appeared in Silurian time, as did also the sharks, and lungfishes followed in Devonian. So abundant and varied were these groups that Devonian is called the "age of fishes." There were, however, no true bony fishes (teleosts) in Devonian, the first of these occurring in Jurassic. By Jurassic time the sharks had exchanged sharp-pointed teeth for flat-topped ones, presumably used for
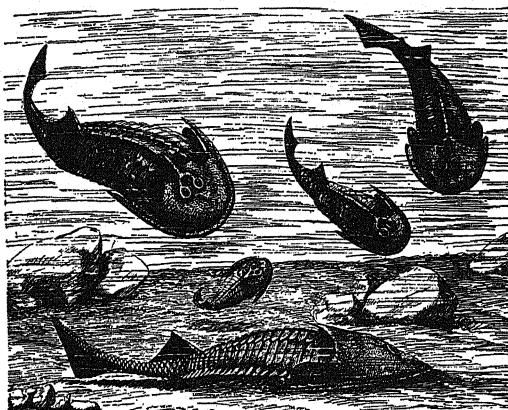
FIG. 45. Small armored fishes, Ostracoderms, from Lower Devonian. (*From Pirsson and Schuchert, Textbook of Geology, John Wiley & Sons, Inc. By permission.*)

crushing shells. Bony fishes gained the ascendancy in Cretaceous, and by early Tertiary they were of the families living today.

Amphibia. The history of the amphibia is so incomplete that the chief reason for including them here is to indicate the extreme difference between the only fossil group that is known to have been abundant and the modern types. By late Carboniferous there were 88 species, belonging to 46 genera. These animals were mostly of the group called Stegocephalia, or similar to them. They possessed a tail, an armored head and belly, and short legs or none at all, and varied in size from a few inches to 10 feet in length. They became extinct in Triassic. Real salamanders, unarmored, date from the Cretaceous. The oldest known frogs lived in the Jurassic of Spain and Wyoming.

Reptiles. The reptiles first became prominent in Permian. Most of them looked like large lizards, some of them with a large finlike projection upon the back. Even more extraordinary was the array of reptiles in the Mesozoic, which has been termed the "age of reptiles."

It is the dinosaurs which are the conspicuous members of the group, owing to the huge size which some of them attained. Not all were large, however; they ranged from the size of a hen to 150 feet in length. The huge bodies bore ridiculously small heads. Some dinosaurs were vegetable-feeders, and these were often horned; they are found only in the Cretaceous. Others were carnivorous, and these were usually hornless. The dinosaurs as a group appeared first in middle Triassic, a little earlier in America than in Europe. By Jurassic they had be-
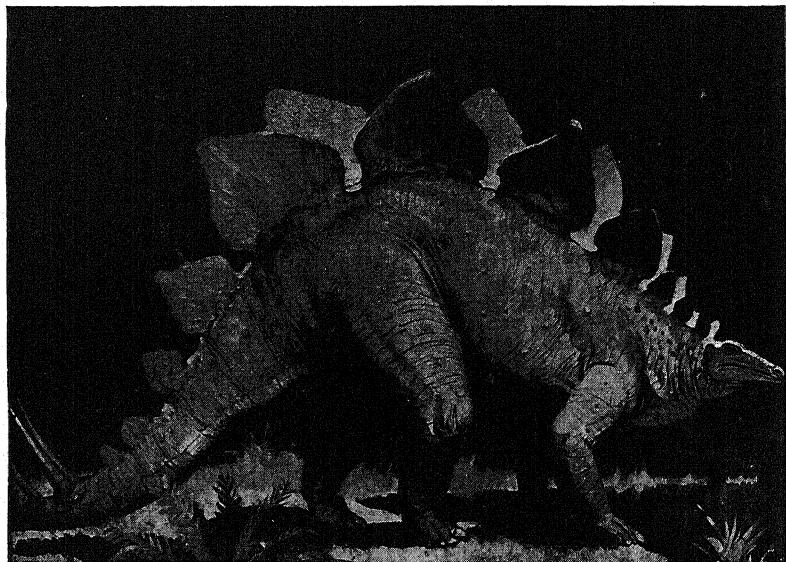
Fig. 46. Jurassic dinosaur, Stegosaurus. (*From Hussey, Historical Geology, McGraw-Hill Book Company, Inc.*)

come very numerous and varied. Armor plates curved over the head and neck; spines, plates set on edge along the back or along the sides (Fig. 46), were common extravagances of structure. Some walked only on their hind legs, the forelimbs being greatly reduced. Mummified skins and dried carcasses show them to have been covered with scales as are modern reptiles. That they laid eggs is shown by fossil eggs discovered in Mongolia. Before Cretaceous many of the large dinosaurs had died out, and very few of the group—none in North America—survived to the Eocene. New groups kept appearing, while the order lasted, for the spoon-billed dinosaurs began and ended in the Cretaceous.

Other curious reptiles of the Mesozoic were the ichthyosaurs, or fish-

lizards, of the Jurassic and Cretaceous; plesiosaurs, marine predaceous swimmers of about the same time; and pterosaurs, the flying reptiles, whose wings consisted of skin stretched between the body of the hand and a greatly elongated fifth finger.

The earliest known turtles and tortoises lived in Triassic time, true lizards first appeared in Jurassic, and the first snakes are found in the Cretaceous. These are the groups that have survived most plentifully to the present time. Tortoises were abundant in Eocene and

FIG. 47. Archaeopteryx, fossil bird of Upper Jurassic. (*Courtesy of American Museum of Natural History.*)

huge in Miocene, and lizards increased considerably in Oligocene. Venomous snakes did not arise until mid-Tertiary.

Birds. The earliest fossil birds are of Upper Jurassic. They had teeth, and their beaks were not covered with horny material. They were like reptiles in these respects, and since some small reptiles were fliers, these Jurassic skeletons are assigned to the birds only because they were accompanied by impressions of feathers. The famous Archaeopteryx (Fig. 47), about the size of a crow, with only a small breastbone (hence not a strong flier), typical perching feet, and no air-filled bones, was the principal representative from that period. Archaeornis, and a feather different from those of both these genera, are the rest of the Jurassic discoveries.

In Cretaceous, Ichthyornis was a strong flier, and Hesperornis a swimmer and diver. These forms still had teeth, though some anterior ones of the upper jaw were missing. A horny bill was also partially developed. A completely toothless lower jaw is known from the Cretaceous of Alberta, Canada.

In Eocene, most of the birds were of modern type. Not many have been preserved from later periods, so that the fossil history of birds is meager.

Mammals. Among the reptiles in the Triassic were some whose teeth were no longer of the unspecialized type characteristic of that group. These teeth showed differentiation approaching that of canines, incisors, and molars (Fig. 48), and there were other differences in the
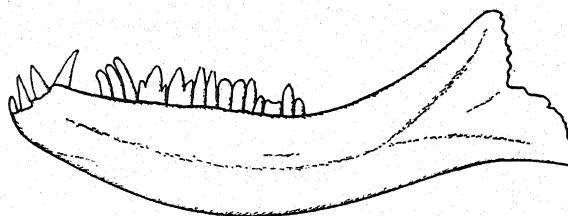
FIG. 48. Lower jaw of mammallike Triassic reptile, showing some differentiation of teeth.

skull which bore resemblance to features of mammals. Such differentiation increased in the Jurassic, and some undoubted mammals, of the size of large rats, existed in that period. Late in the Cretaceous were two types whose skulls resemble somewhat those of opossums and shrews. Through the whole Mesozoic, however, mammals were subordinate to the reptiles.

Then followed the great development which made the Cenozoic the age of mammals. It brought a succession of forms which for size and sheer oddity almost equaled that of the Mesozoic reptiles. Seven orders of mammals are known from the Paleocene, and a few of these groups survive; the American opossum (Fig. 27) of today has changed little from its primitive appearance. Rapid changes took place, however, in Eocene time. The huge uintatheres (Fig. 49) with their curious head protuberances and curved tusks were very common. Other mammals were the horse and camel ancestors, the rodents, rhinoceroses, primitive elephants, and primitive monkeys.

Only a few of the later developments can be given in this brief account. The saber-toothed cats, with their 6-inch flattened upper canine

teeth, must have been a terror around the water holes which other animals had to visit. They lived in temperate North and South America in the Pleistocene period. The ground sloths were giant immigrants from South to North America in Pliocene and Pleistocene. They must have walked clumsily on the outer edges of their feet, with their long claws bent inward. Some huge armadillos, also northward migrants from South America in Pliocene and Pleistocene, reached a length of 14 feet. Rhinoceroses that could run with agility existed in Eocene
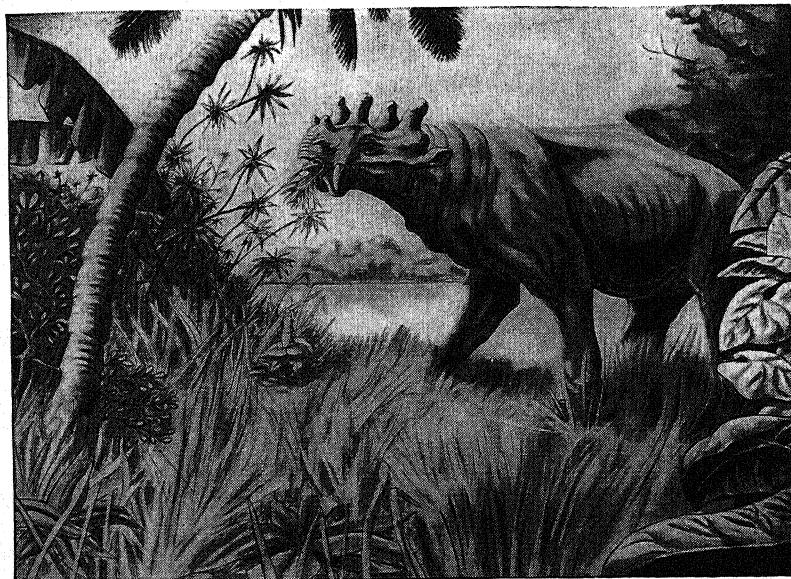
FIG. 49. Eocene uintathere from Wyoming. (*From Hussey, Historical Geology, McGraw-Hill Book Company, Inc.*)

and Oligocene, while another rhinoceros of the Oligocene and Miocene of Asia grew to the largest size of any known mammal—25 feet long, 13 feet high at the shoulders. A deerlike animal with protuberances on the front part of its nose as well as horns on top of its head is found in the early Miocene of North America.

These curious examples are but a few of the strange creatures which made up the group of mammals during Tertiary time. In late Pleistocene they experienced a drastic and mostly unexplained destruction. Perhaps the glaciers had something to do with their disappearance. Seldom in geological history have there been comparable exterminations of great groups. Only the tropical regions, notably Africa, escaped

this great destruction, and Africa's Pleistocene mammals were essentially like those of today.

The Tree of Horses. Omitted from the foregoing story are several series of changes which are especially convincing as evidences of evo-
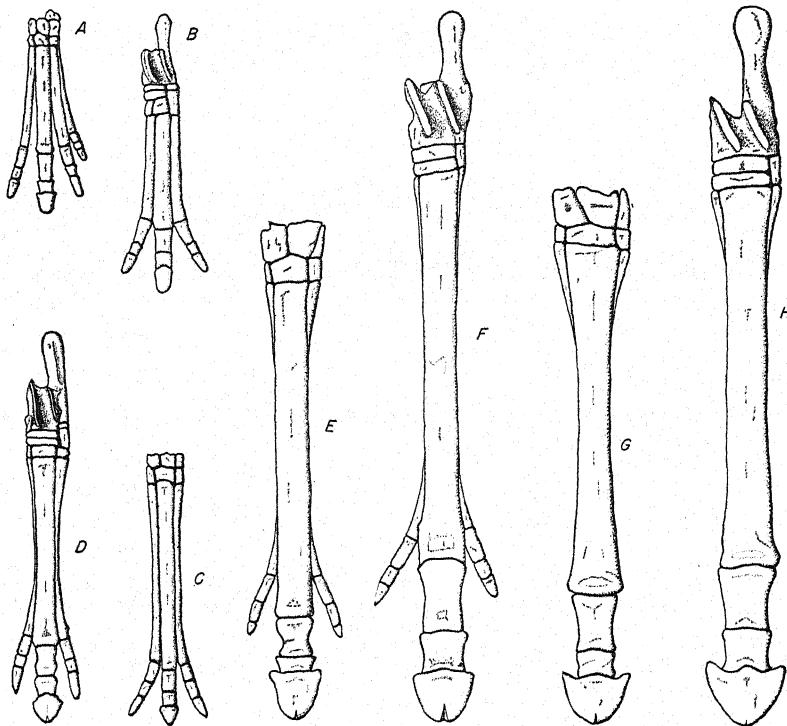
FIG. 50. Forefeet and hind feet of fossil horses. A, B, Orohippus; C, D, Mesohippus; E, F, Merychippus; G, H, Equus.

lution because the steps involved are small. A classical example is that of the horse.

The first mammal now recognized as horselike was Eohippus, or its near-equivalent Orohippus, in the Eocene. These animals were scarcely a foot high, had an arched back (not the sagging one of the modern horse), and had four digits on the forefeet and three on the hind feet (each digit ending in a hooflike nail). Their molar teeth had hills and valleys on their functional surfaces, which prevented them from slipping sidewise on one another. Such animals could not therefore eat grass, which can be sufficiently broken up only by a grinding

movement; they must have eaten twigs or other vegetable matter thick enough to be crushed by mere pressure. The molar teeth also had roots that were longer than the height of their crowns.

Successive horselike animals differed from these Eocene forms in size, in the number of toes, and in the characters of the molar teeth. Four types, belonging to different geological periods, are ample to illustrate the difference.

The increase in size, to that of the 5-foot modern horse, is reflected in the sizes of the feet in Fig. 50, where all types are drawn to the same scale. The toes are reduced in number, first to three on each foot in Mesohippus (Oligocene) with the lateral toes still partly functional, then to three with only the middle one functional in Merychippus (late Miocene and early Pliocene). The genus Equus, both in Pleistocene fossils and modern horses, has the lateral toes still further reduced to splint bones.

In the form of the molar teeth, Merychippus is transitional. Before it, the surfaces of the molars were rough; in Merychippus they were flattened enough for grinding movements; and in Equus the flattening is accentuated. In Merychippus the length of the roots and the height of the crowns are about equal; before it the roots were the longer, after it the crowns were the longer (Fig. 51).

The members of the horse series have been found mostly in North America, but the line became extinct there long before the coming of white men to this continent. Horses had migrated to Europe, however, and their descendants were brought back to the Americas as domesticated animals. Wild horses are the descendants of some which escaped from domestication or were abandoned.

Other Mammals. Some of the changes characteristic of the horse have parallels in successive fossils of other mammalian types. Increase in size has been fairly common. Such increase occurred in the camel and elephant series, the only others to be considered here. Molar teeth with merely crushing surfaces have often been succeeded by grinding (flat-topped) teeth; this is true of camels and elephants. The number of toes decreased in the camel line, but only from four to two. A striking change in the teeth of elephants is the conversion of the outer upper incisors to tusks weighing several hundred pounds in some forms. The great weight of these tusks requires greater leverage for the muscles of the neck, and this is provided by greater height of the base of the skull, attained by added amounts of spongy bone.

The history of the "camels" refers to the camel family, which embraces not only the Arabian one-humped dromedary and the Asiatic

two-humped camel, but also the llamas and alpacas and their wild
ancestors of South America. The camel family began in late Eocene
in North America, mostly the United States, which has none of them
now except in circuses and zoological gardens. No other continent re-
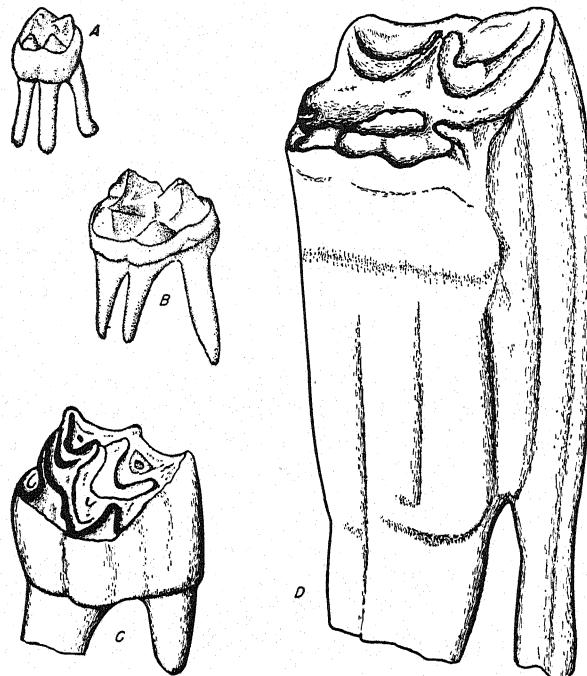
FIG. 51. Molar teeth of fossil horses. A, Eohippus; B, Mesohippus; C, Merychippus;
D, Equus.

ceived any of them until Pliocene time—at least none has been pre-
served and discovered.

The story of the elephants is strictly African through Eocene and
Oligocene. Then these animals spread to Europe and Asia, even to
North America, in early Miocene. In this continent they were the
mastodons, whose skeletons are still being discovered.

For the details of these and other mammalian lines—or those of other
animals—reference should be made to works emphasizing the course,
rather than the causes, of evolution.

Significance of Fossil Series. The advantage of such series as those
of cephalopods, horses, camels, and elephants, as indications of evolu-
tion, is that the successive changes are small. It is a weakness of

paleontological evidence that a genetic relationship can never be directly proved. However reasonable it may be to assume that one fossil type descends from another, or that two contemporary types are cousins, that is still an assumption. Biologists assume these relationships when they can see the similarities which seem to justify such a conclusion. They are doubtless joined by nonbiologists when the similarities are as close as those between living Nautilus and the fossil coiled nautiloids, or between living brachiopods and fossil Lingula. But when the layman is presented with the little elephantlike Moeritherium and a modern elephant, or with Eohippus and a living horse, he could be pardoned for some doubt concerning the genetic connection between the two. Here is where the *series* is of importance; the large gap is divided into a number of small ones. The difference between nautiloids and goniatites is small; they obviously are similar animals. Mesohippus differs only moderately from Eohippus, and Merychippus helps to bridge the gap from Mesohippus to Equus. No one but a biologist would quickly see the similarity of an ammonite to an orthocone; others might question whether one type could be a descendant of the other.

When, however, these large differences are broken up into a succession of small ones, by the occurrence of forms intermediate in structure and in time, there is no difficulty in seeing the presumable connection. Goniatites and ceratites give plain indication of a common source, as do also Merychippus and Equus, if the theory of homology is accepted at all. Similar arguments concerning relationship may be derived from the human tree, which is presented by itself in the following chapter.

ORIGIN OF MAN

> . . . the most important . . . change distinguishing man's
> evolution has been the development of his brain power . . . this
> increase of brains . . . became . . . adequate for . . . the
> continued development of tradition, whereby . . . learning by
> experience was enabled to unite the experiences of coexisting in-
> dividuals and extend over countless generations . . . the better-
> ment and increase of tradition itself . . . may be largely
> summed up in the word "science."
>
> —H. J. MULLER, 1949

While the discovered human tree is not one which would be ad-
duced to prove the occurrence of evolution in general, it is good
enough to carry conviction when considered in conjunction with proof
of that process in other branches of the animal kingdom. The account
of man's origins in this chapter is designed to be an appendix to the
story of fossils in the preceding one. Accordingly, the pertinent fea-
tures of fossil creatures approaching in their characteristics the men
of today are to be emphasized. That means pushing aside the plain
homologies between man and the apes. Before fossil men or manlike
animals had been discovered, the anatomical similarities of men and
the other living primates had been carefully studied. Homologies had
been deduced, and that meant common ancestry. A probable ancestor,
common to man and the apes, had been visualized. While comparative
anatomists differed in their ideas of this ancestor, a common conclusion
has been that it resembled the extinct apes of the genus Dryopithecus.
Such an ape could have given rise to the chimpanzee, orangutan, and
gorilla, as well as man. Even when a somewhat different ancestor is
pictured, it is always conceived to be the progenitor of all the present
great apes and modern man.

What Is a Man? If man's relationship to the apes is correctly con-
ceived, even approximately, the task before us is to sort out the dif-
ferentiating characteristics and discover how and when they arose.
Also, if tracing the origin of man is a goal, we need to know when we

have arrived. What does it take to make a man? Among the features of man today is his erect posture. He has a thumb which may be opposed to each of the fingers, but the great toe cannot be so manipulated; the hand is thus a grasping organ, the foot is not. Man uses tools. The grasping hand probably has something to do with the tool-using habit, but more important is the intelligence which tells how to use tools. The intelligence comes from concentration of the nervous system —plus other things—and part of the concentration is in a large brain. Man has a voice, and sounds have become symbols of things; that is,
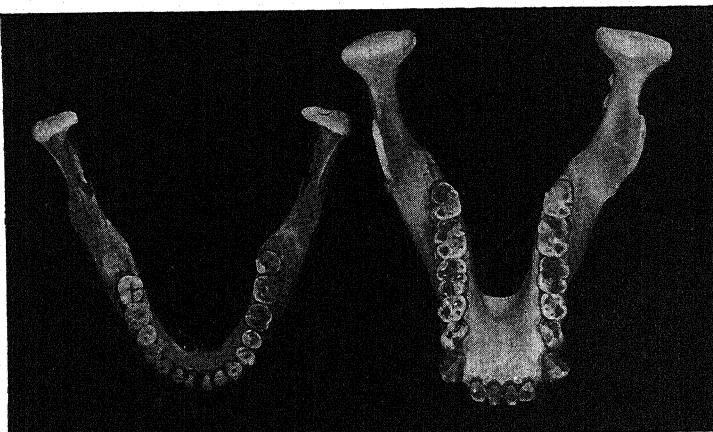
FIG. 52. Lower jaw and teeth of modern ape (*right*) and modern man, showing shape of row, and relative dimensions and number of cusps of molars. (*Courtesy of Dr. William L. Straus and Quarterly Review of Biology, Williams & Wilkins Co.*)

man speaks, has a language. His body has certain proportions, and the appended limbs have certain relative lengths.

Voice and language are not preserved in fossils, and it is uncertain whether any of the very early creatures we shall be examining had them or not. The anatomical features, however, are known to the extent that the pertinent parts have been found. When a being is discovered that possesses most of the above-listed characteristics at least approximately, it is fair to assume that we have found a man. Even if we disagree as to what is a man, we still can trace the origin of *modern* man; and the process is still the sorting out of man's and the apes' characters.

Contrasting Features of Apes and Men. Enough of the distinguishing marks of apes and men should be known by the general student to

enable him to understand the problems of the anthropologist. The size of the brain can be determined roughly from the volume of the skull cavity. Even fragments of the curved skull bones enable a less accurate estimate of cranial capacity. Since the largest ape, the gorilla, has a cranial cavity of about 600 cc., the smallest modern man over 900 cc., and the average modern man 1320 cc., there is room for intermediates which might indicate a course upward toward man. Prominent brow ridges over the eyes characterize the apes, while those of man are scarcely noticeable. Man's forehead is high, the ape's sloping. The human lower jaw has a prominent chin, the ape's a rounded tip. The rows of molar teeth in man diverge from one another backward, making the arch roughly a parabola, while in apes the molars are in nearly parallel rows so that the arch is a long narrow U (Fig. 52). The crowns of the molars in apes are longer than wide—length is measured along the jaw, width across it—and they have five cusps on their surfaces; human molars are nearly square and mostly have only four cusps. These features are also visible in Fig. 52. The canine teeth of apes project beyond the level of the other teeth; those of men do not. The arms of apes are relatively longer than those of man. This relation is shown by the femur (thighbone) and humerus (upper arm) of the chimpanzee (Fig. 54, A) and their homologues in man (C). The two bones are of about equal length in the chimpanzee, while in man the femur is distinctly the longer.

These distinctive features will not always be mentioned in describing human or prehuman skeletons, but they were in the minds of the anthropologists who reached conclusions concerning those skeletons. There are other differences between apes and men, and when these are important they will be described at the points where they have a bearing.

The Java Discoveries. The oldest fossils showing an advance toward man were found on the island of Java. A Dutch army physician named Dubois uncovered the first fragment in the year 1890. He had set out to find evidences of fossil man there without having any advance tip, from industrial excavations, that such bones were there—one of the few instances in which unguided excavations have paid off. His finds within the next year or two included a skullcap, a lower jaw, two separate molar teeth, a premolar, and a femur. Dubois regarded the possessor of these bones as the missing link, and called him—or her —*Pithecanthropus erectus*. No other anthropologist was permitted to see the specimens until 1923, so that Dubois's descriptions were the only information on which judgments could be based. Naturally there

was controversy. Some doubted whether the parts all belonged to-gether, particularly the femur, which was 50 feet away from the head parts. The brain cavity is estimated at 914 cc., which is intermediate; the jaw and teeth are partly apelike. There was thus room to think of the skull and teeth as presenting a disharmony, and some anthro-pologists thought they did.

Then other discoveries were made in Java, partly by Dubois him-self, under the aegis of government agencies or research institutions, beginning in 1931 and extending to 1941. The war prevented further efforts. As a result of such studies a number of other places in Java yielded bones (see map, Fig. 53). Some of these bones were practically
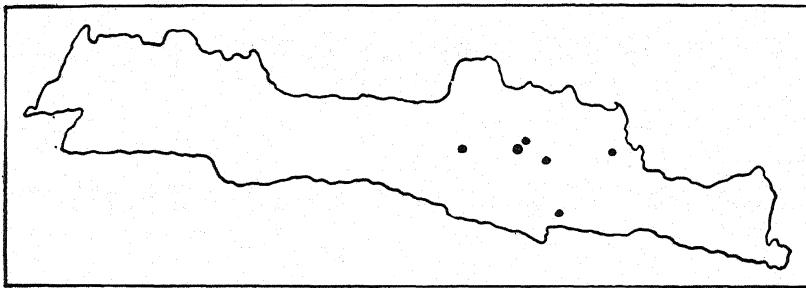
Fig. 53. Outline of Java showing places where early men have been found. The largest dot is Trinil where Dubois made the original discovery.

identical with Dubois's original specimens, but two of them were more advanced types. At least one of these two was plainly of a later geological time. The original find has most often been allocated to mid-Pleistocene, perhaps half a million years ago, though there is some disagreement. One anthropologist, Weidenreich, is sure that the two advanced types, with the more primitive ones, form a connecting series —a human line—leading straight from Pithecanthropus to the natives of Australia.

Perhaps we may go backward, as well as forward, from Pithecan-thropus. In 1941 a *giant* lower jaw with three teeth in it was discovered by von Königswald, a German anthropologist, at Trinil, near the place of the original find by Dubois. It was named Meganthropus from its size. One of the other skulls from Java was large, but not equal to this new one. The other features of the various Java skulls appeared to show that the larger ones were the more primitive. Accordingly, Weidenreich is prepared to assume that the giants were ancestral to the smaller people—hence ancestral to the Australian natives. He

points out that gigantism has occurred in other groups of animals. Unfortunately for this argument, the huge mammals of the Tertiary were not the progenitors of the smaller mammals of today, nor have the small reptiles of the present come from the dinosaurs. Large size in these groups led to a blind alley, not to the races of the future. Still, the position of the giants of Java as heads of the human family is not thus disproved.

That gigantism was not just a Javanese phenomenon is indicated by the contents of apothecaries' trays in South China. "Dragon bones" (fossils) are valued as medicine there, and common people know where such things can be found. It is a practice of anthropologists going to China to visit these drugstores first to get clues as to what they may expect to find. Sometimes the supplies in these shops are all they ever do discover. Several teeth obtained in this way have been interpreted as human molars, though they are five or six times as large (in volume) as molars now are. How big these Chinese giants were there is no way of telling, since correlation between tooth size and body size has not been ascertained. Weidenreich holds that they must have been larger than the giants of Java—and ancestral to them. So, according to him, it was the giants of South China that produced, eventually, the modern natives of Australia.

Peking Man. The Chinese giants are of special interest because of the human fossils discovered near Peking. Beginning with a couple of teeth in 1926, later a lower jaw, the discoveries were climaxed by a number of skulls, the first in 1929. The site was a partially collapsed cave used as a dwelling near the village of Choukoutien—a name commonly used by anthropologists rather than Peking. Four of the skulls are fairly complete, and there are many teeth, a few pieces of thighbones, fewer still of the armbones, part of a collarbone—and not much else. What sort of being do these parts represent?

The average brain capacity was about 1075 cc., greater than that of Pithecanthropus and about equal to that of some modern savages. The few long bones indicate a height of about 5 feet, a little smaller than Java man. The teeth are large and show no signs of decay. The arm and leg bones have had to be reconstructed; hence their lengths are not too accurately known; but it seems certain that the arms were somewhat short, in relation to the legs, as compared with modern apes, but not so short as the arms of modern men (Fig. 54).

Weidenreich considers Sinanthropus (another name of Peking man) the same sort of being as Pithecanthropus—not as the two more advanced types from Java—so that details may be spared here. He regards

these men as descendants of the Chinese giants, and in turn as the ancestors of some of the modern Mongoloids of China and elsewhere. That might also make Sinanthropus the ancestor of the Eskimos and American Indians of the New World, as we shall see later.

Several Puzzling Men. There are several men, more advanced than those of the Orient just described, which have a more definite relation to the evolution of anthropology than to the evolution of man. They have been the subjects of much controversy, and of great doubt
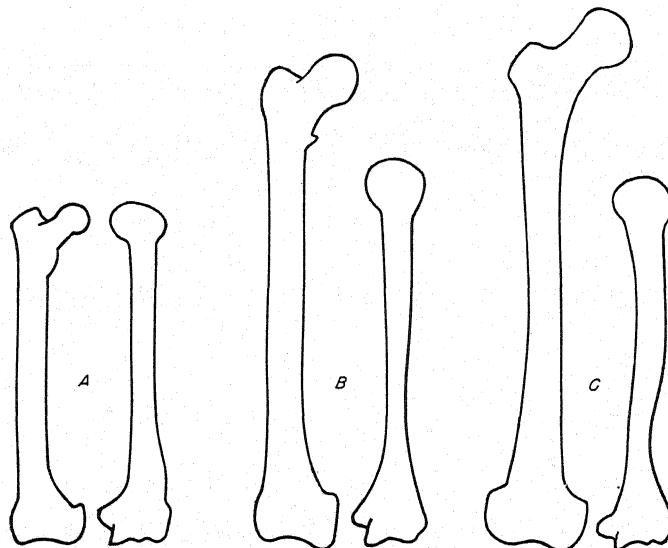
FIG. 54. Humerus and femur of (A) chimpanzee, (B) Peking man, and (C) modern man, to show progressive relative shortening of the arms and to indicate relative stature.

on the part of those not participating in the debate. One of these controversial beings is Piltdown man, so named from the common in southern England where the parts of a skull and a lower jaw were found in 1908. The geological time is a bit uncertain because the bones were found near the surface, in material that might have been moved. Other bones near it might also have been moved. The skull was strictly human, except that the curved bones were too thick, while the jaw was mostly apelike. Most anthropologists thought they belonged together and that the disharmony of the skull and jaw was just one of those things which evolution could do—change one part of an animal earlier and faster than another part. There have always been,

however, eminent dissenters. Even the size of the brain cavity was in doubt, since Smith-Woodward estimated it at 1070 cc., Keith at 1500 cc. Weidenreich concludes that the skull is completely modern and that the jaw could not possibly belong with it even if the two had been found side by side. It seems unsafe, therefore, to reconstruct any part of human evolution on a foundation involving Piltdown man.

Another center of controversy is Rhodesian man, from South Africa. The find consisted of a skull, nearly complete but without a lower jaw, some leg bones, and parts of the pelvic girdle. Disharmony of the skull parts again created a puzzle; for the face was protruding and the brow ridges heavy like an ape, while the cranial capacity was a good human 1300 cc. The stature was about 5 feet 10 inches. Dating discoveries from other fossils in Africa is difficult, for fossil African animals back through the Ice Age are pretty much like modern ones. Those best qualified to judge Rhodesian man place him in a group of primitive Neanderthal people, and therefore more properly considered in later sections. His disharmonies, however, render this opinion of uncertain value, and he is omitted from further consideration.

The Heidelberg man, found near Heidelberg, Germany, in 1907, is known only from a lower jaw. The massiveness of the whole structure, teeth and bone, would make it a fairly good ape. Yet his teeth are human in form; they are small for the bone in which they are set, but larger than modern human teeth. One guess is that Heidelberg man was an ancestor of the Neanderthal group and that he lived in the second interglacial period.

These three types have figured extensively in discussions of human evolution, but have not thrown much light on that process.

Neanderthal Races. With the advent of Neanderthal men, briefly referred to in the preceding section, the work of the anthropologist was lightened in one respect—more fossils were available for study. Yet it was more difficult in another way, because the many fossils did not completely agree. More than a hundred individuals have been recovered, at least in fragments, and some of them are nearly complete. The first discovery of this type was made in 1856, in the valley called Neanderthal, near Düsseldorf, Germany. Note the date—1856—for at that time the evolution idea was not yet generally accepted even for other organisms than man. It is not surprising, then, that the bones uncovered in digging limestone for commercial kilns did not at once arouse interest. Eminent scientists dismissed them as pathological, or at least aberrant variations. The same lack of interest is shown by the fact that a skull of the same type had been found at Gibraltar

as early as 1848 but was not considered important in any respect. Only in the 1880's did these fossils begin to stir any excitement. By that time Darwin had startled the intellectual world by his studies of the origin of man. After that many discoveries were made, mostly in caves where Neanderthal man lived and where he buried his dead. This burial is what made the finds so numerous and the skeletons so nearly complete. Nearly every country of western Europe and some in the Near East have furnished specimens. None has turned up in England, however.

The skulls had heavy brow ridges, and the face was protruding. The nose was wide, the chin nearly lacking (Fig. 55). Cranial capacity was high, ranging up to 1600 cc., which is above the average of today. Though the stature was only around 5 feet—more for men, less for women—the build was stocky. The lower leg was short, compared with the thigh, and this is taken to mean that Neanderthal man was a clumsy, slow-moving person. Fleet people generally have long shinbones and short thighbones.

The time of these people was the latter part of the third interglacial period and the advancing stage of the fourth glacial. That may have been 100,000 to 70,000 years ago.

Tools are found in many of the caves where bones are recovered. True, these are not the first signs of culture, for tools of the chopper tradition were found with Peking man's bones. But with Neanderthal remains the tools were so numerous as to give a real idea of how men lived. They belong to the Mousterian culture, so named from Le Moustier in the Department of Dordogne, France, where tools were found in 1869 unaccompanied by skeletons. Forty years later a Neanderthal skeleton was also found near Le Moustier. The tools are of flint (Fig. 56), in the flake tradition. There were also some bone tools. The flaked tools are not too hard to make; modern men have made them just to show they are as good as their Neanderthal forebears or cousins. On the whole, and after taking into account their background, one must regard men of that period as rather capable human beings—perhaps as good as the politicians of today by whom people who do not agree with them are labeled Neanderthalers.

The Fate of Neanderthal Men. What became of these Neanderthal folk? Up to the late 1930's the general opinion was that they had been driven out or exterminated suddenly by invading hordes from the East. That does not seem likely. Conquering invaders even in barbarian ages have not usually exterminated their victims. They preserved the conquered women—at least the more attractive ones—and the racial characters would be transmitted as well by the women as by the
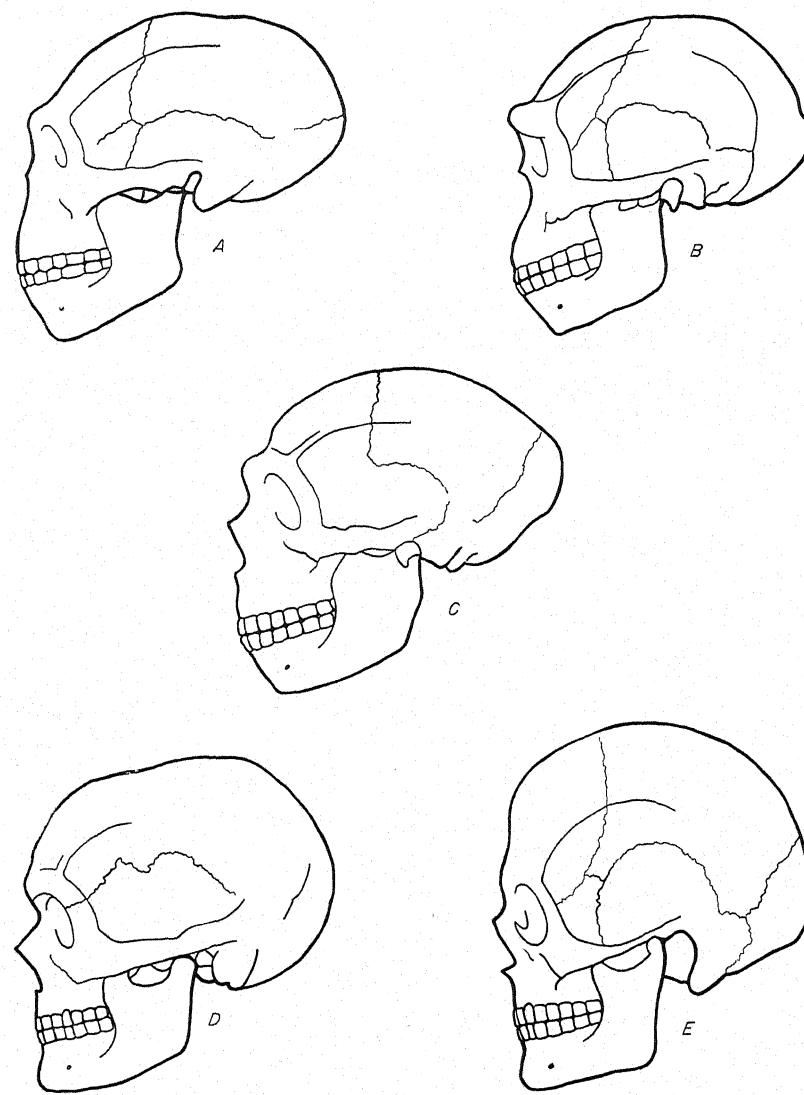
FIG. 55. Skulls of (A) Pithecanthropus, (B) Sinanthropus, (C) Neanderthal man, (D) Cro-Magnon man, (E) modern man.

men. The racial hybrids thus produced should show some intermixture of Neanderthal characters with those of the conquerors, or intermediates between the two, depending on the mode of inheritance. The difficulty was that such mixtures or intermediates between Neanderthal and modern men were not known. Moreover, Neanderthal man lived in Europe until the height of the fourth glacial period. Invaders would hardly have been interested in seizing the lands of other people living under the hard conditions of glacial time; they were more likely to take areas with mild climate.

Mount Carmel. Then in 1931–1932 two caves on the slope of Mount Carmel, near Haifa, Palestine, were found to contain bones and tools of people—down to a depth of 50 feet in one of them. That depth indicated long occupation. These people—10 were found—were interme-
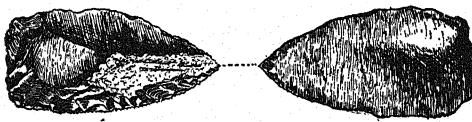
Fig. 56. Mousterian point and scraper, the two sides of one implement. (*From Hussey, Historical Geology, McGraw-Hill Book Company, Inc.*)

diate between Neanderthals and modern men. Since they were contemporary with Neanderthal men, they could either be representatives of an evolutionary change toward the present types, or they could be hybrids. The latter would require that a type more advanced than they be already in existence somewhere.

The tools found on Mount Carmel were nearly uniform in type, not mixed as tools so often are. At the level where the skulls were found, there were some thousands of tools, and almost all were flake products. The oldest blade tools known were recovered from the bottom (early) deposits in these caves.

The anthropologist Keith believes the Mount Carmel group must be placed directly in our ancestral line. This would probably mean that the Neanderthal people had been absorbed, not exterminated, and that their blood is now in part our own. Krogman also is convinced that modern man evolved from Neanderthal. It is not a bad heritage.

Modern Man. It has been customary to label the next step in human evolution Cro-Magnon. But the people so named were of completely modern type. They were big—6 feet tall—and had large heads (larger than most of ours) and high foreheads (Fig. 55). Apelike characters had all disappeared. No brow ridges were observable; the chin was

prominent; the face did not protrude. Shoulders were broad, chests deep. The lower leg had lengthened, relative to the thigh, which probably means these men were active and speedy, unlike Neanderthal.

The name comes from the locality in Dordogne, in southwest France, where in a cave the first skeletons of this kind were found. With them were the bones of wild animals, mostly broken open, probably to get at the marrow. Stone tools, necklaces of shells, and carved ivory figures were found in various caves, later assigned to what is called Aurignacian culture. There are some people still in Dordogne who measure up to the Cro-Magnon physical standards, others like them in the Canary Islands. It is possible they are little-changed direct descendants of the men of the French caves; the French anthropologist Boule thinks they are. Men of today have themselves in general liked the idea that they were descended from Cro-Magnon.

Our descent from the big men first called Cro-Magnon would, however, involve a regression in size of both body and head for most of us, and paleontologists have generally held that evolution does not retrace its steps. It should not be actually impossible for a line of descent to return to a former state, but in view of changed conditions and the many other things which evolution could do, it has seemed unlikely that there should be any such return. Besides, observed reversals in actual fossil series are lacking.

This conclusion does not, however, leave us without ancestors, for contemporary with the big men of Cro-Magnon were many others of smaller size. They were well scattered in western Europe. While some writers include these smaller men in the Cro-Magnon group, only confusion can come from that practice. One anthropologist puts most of these contemporaries of Cro-Magnon into a group called the Combe Capelle-Brünn. Many specimens are available. An important feature of them is that they were not all alike. Just as there are many kinds of men today, yet all of them men, so there were different kinds of men in the Combe Capelle and Brünn type. Even when only a few thousand men lived on the whole earth, they were presumably of different sorts. The variety shown by these contemporaries of Cro-Magnon pretty well bridge the gap between Mount Carmel and men of today; and, as we have seen, Mount Carmel formed an approach to that bridge from Neanderthal.

Cave Art. Evidences of culture have been used only sparingly in the story of man's rise, since culture may have little to do with biological evolution. You do not need to be smarter than the preceding generation in order to know more than it did, for you have learned from it

and can go on from there. Tools throw much light on modes of living, but may mean nothing in the development of races. It is a popular notion, however, that art is in a different category, that it implies a mental—an aesthetic—quality not exactly connected with problems of living, and hence that it indicates one of the things that make men men. Ivory figurines have already been mentioned. In the caves of early modern men, notably those on either side of the border between France and Spain, are numerous paintings. The best of these are said by some students to "compare favorably with the best art of any time."
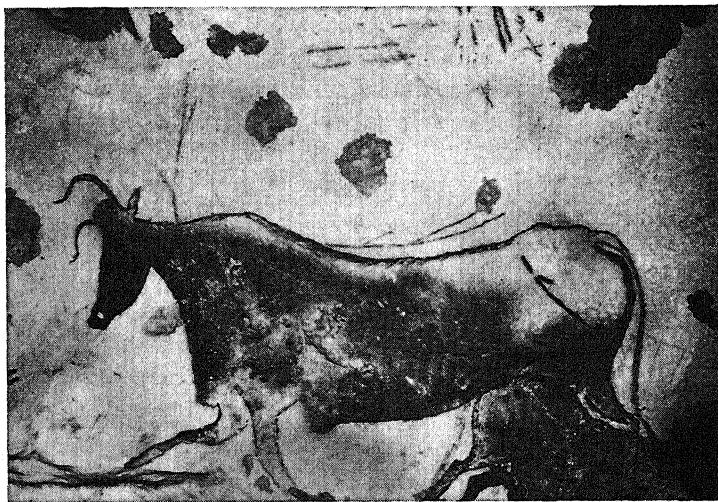
Fig. 57. Painting of animals on walls of cave of Lascaux in France.

When allowance is made for a tendency of critics to praise the old and decry the new, a fair judgment by a layman would probably be that some of the old art is good, some not so good. Certain of the pigments used were of a quality which modern paint might well copy if their secret could be learned.

What is the significance of this art? The subjects of the paintings were mostly animals (Fig. 57). They were put on the walls and ceilings, not of the front parts of the caves, near the entrance, where people lived and where the pictures would be often seen, but in the deeper, darker recesses. Only such light as was furnished by crude lamps burning some kind of fat would have enabled the artist to do his work. Attention has been called to the fact that some paintings were obliterated by putting new ones over them. Painting over old pictures

has been done in modern times, too, but scarcity of canvases has been given as the reason; or the motive might have been something else. In the caves, even if already-occupied walls were the best ones, or the only good ones, putting a new painting over an old one is thought to indicate that the value of art then was in the act of producing it, not in looking at it in satisfaction of an aesthetic sense.

A number of anthropologists have guessed—guessed is the right word—that this old art was somehow related to magic. The animals painted were mostly game animals. It is suggested that, in painting these beasts, the artist imagined that he was gaining some sort of con- tral of or advantage over them. Perhaps he thought that he could the more easily capture or kill them, once he had painted their portraits. When male and female are included in the same picture, the suggestion has been that somehow he thought this would help increase the numbers of game animals.

Cave painting is thus regarded as primarily an economic matter. That should not be surprising, for some features of modern art are plainly economic rather than aesthetic. Still, early modern man was using a method of expression which his forebears did not use. We feel pretty sure that some modern men have an aesthetic sense, and there is no reason to believe that most beasts have enough of it for us to detect it. That sense must have originated, or increased, sometime. The early modern cave period would not have been a bad time for such origin or increase.

Agriculture. The people so far described found their food already produced. They moved about to get it, as the supply changed. Part of this moving was seasonal. In Europe, they lived in caves in winter, in the open and traveling in summer, returning to caves—perhaps not the same caves—the next winter. Game animals were followed, plants that furnished food had to be sought where they grew. No one thought of producing food, or at least no one acted on the idea.

The need for producing food can be portrayed more easily than the steps by which such production was adopted. Man must have multiplied in number if conditions permitted, while the natural food supply may already have reached an equilibrium. Moreover, with the retreat of the glaciers the types of game animals changed; smaller animals prevailed. One kill did not last so long. How domestication of animals and the planting of crops arose can only be guessed. The first animal to be domesticated was the dog, and it was not used for food; it was doubtless more useful in other ways—anyway, it was probably not too palatable. But the idea of domestication was thus planted, and

other animals were found which could be herded. The meat supply, on the hoof, thus became more durable than the flesh of large animals occasionally killed. That plants came from seed must have been observed, and the mind of man in need of food could hardly escape the idea of planting those he could use.

The last people we know much about who were still just food collectors possessed the culture known as Natufian. They are represented by the upper deposits in the caves of Mount Carmel. Perhaps their date would be about 10,000 B.C. Some of the flint tools of these people were blades, and a peculiar polish on the cutting edges of some blades is believed to have come from cutting grasses with them. The grasses need not have been raised; they could be wild; but man was harvesting them. In the caves were found fragments of mortars and pestles, which might have been used for grinding food; but the food could have been merely harvested, not raised.

Villages. With the production of food, it was possible for more people to live together. These people could stay in one locality, so it was worth while to build houses. Anyway, the caves were probably at a distance from the best tillable soil. So villages were established. The earliest-known villages are those of a fertile strip extending from the Nile Delta through Palestine, Syria, and south Turkey, and far into Iran (Fig. 58). The oldest of these villages is in the eastern part of this strip, and the younger ones are successively to the west of it. These villages are regarded as dating from about 8000 B.C.—later, rather than earlier than that. In them are found the things which indicate agriculture, things the Natufians did not have. In the oldest of them were hoes, stone devices for grinding grain, and remains of sheep and goats. There were other signs of advancing culture, but we are interested in the signs of food production. The later villages to the west show signs of cattle, bins for grain storage, and in the Nile Delta actual grain. Perhaps the dry Egyptian climate is responsible for preserving the last of these items.

The dates given for the food-collecting Natufian culture and the oldest of the agricultural villages leave a gap of a couple of thousand years. The extent of this gap, in the anthropologists' calculations, is partly determined by the time they think would be required to bring about the changes which the villages show. It is difficult to assign dates without relying heavily on such estimates, though radioactivity tests now being made should help. The 2000-year gap is being filled in by new discoveries, but until the studies are complete the results can hardly be evaluated. The contemplated reduction of the gap

is mostly at its more recent end, that is, a village a little older than the ones mentioned above is being studied.

Agriculture developed also in other areas than the Near East. It came a little later in Europe, hence was presumably transplanted thither, partly through Turkey and Greece and up the Danube Valley, partly along the Mediterranean (by boats) or through North Africa and across to Europe (again by boats) including the British Isles. The ancestors of the American Indians started their agriculture a little
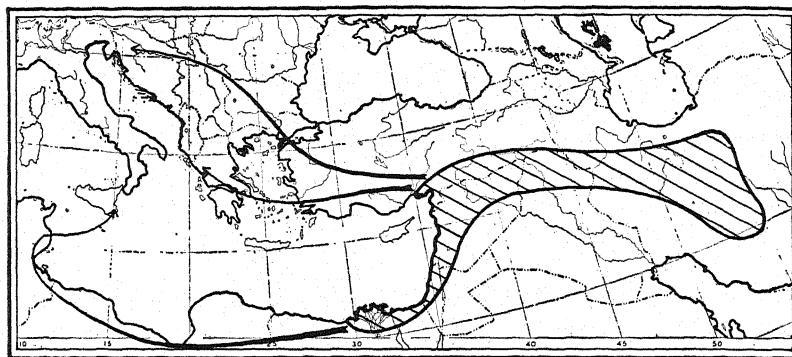
FIG. 58. Highly fertile area (shaded) of the Near East in which agriculture began and the first villages were built, and the paths (arrows) along which agriculture may have spread into Europe.

later than the Mediterranean group, but quite independently of the latter. How and when China started cannot yet be told.

Culture and Biological Evolution. Since this book deals primarily with biological change of species, it is important to make clear the relation of changes of human culture and that evolutionary process. Cultures of men have not been brought into the account merely because of their human interest, though perhaps it would be justifiable to introduce them solely for that reason.

As a long-time and generalized process, the development of culture must be in part dependent on racial characteristics. All races and tribes of men have their culture of some kind, while the beasts can scarcely be said to do so. There must be something in the genetic constitution of mankind to make culture possible, even inevitable. When, however, one considers the changes in culture that arise in a given line of descent or in successive generations of one group, it must be emphasized that such cultural changes do not have to be preceded by corresponding biological changes. People—some people—get ideas

at intervals, ideas of new things to do or new ways of doing old things. They may act on their ideas and start a new practice. Other people who do not get ideas may nevertheless see the advantage of the new practice and adopt it. Fashions grow in that way. Later some one gets another idea and does something differently, and a new fashion in doing things is set. No one knows what gives people ideas. Most people get ideas, some better than others, though not all may act on all of them.

An important feature of ideas is that they differ at different times. They always depend on what has gone before. No one gets an idea of improving a wheel before there has been a wheel. No one has an idea for improving a calculating machine unless there has been a less perfect machine before. The man who improves a wheel or a machine may not be any better than—perhaps not as good as—the one who invented the earlier product. He has had the advantage of experience with the imperfect device. Ideas change with age; a man of fifty seldom gets ideas like those he had at twenty, though he is inherently exactly as capable as he was before. There are many evidences that men in the United States today are not fundamentally superior to the men of 1870 before our industrial revolution really got under way; but they have very different ideas about the way to run a factory. Cultural evolution does not presuppose biological evolution, and students of evolution should be careful not to mix the two so as to infer the latter from the former.

While biological evolution need not control social evolution, the tables could very well be turned. Cultural evolution may possibly alter the course of biological evolution. It would do so by preserving different types. Relative values of human traits change as social practices change. One of the easiest ways to illustrate this principle is by that part of a culture which involves medical practice. Among old tribes, a man would better be healthy; the medicine man could not help him much by incantations. Today there are certain diseases which a man might about as well have as not, as far as he himself is concerned, since these diseases are under control anyway. There are numerous defects now which are not so serious as formerly, because social practices tend to nullify them. Civilized man is probably evolving himself downhill by social practices which he regards as right and good.

The relation of cultural to biological evolution thus appears to be lopsided; cultural change affects, more than it is affected by, biological change. Whether this differential is any less than it seems may be debated. There is a popular view that it *is* less. It is sometimes claimed

that certain peoples do not have the mechanical genius to manage big industrial developments. It is said they can copy, but not create. They can build, but not invent. They cannot improvise. When the statement is made concerning an actual or a potential enemy, it is readily believed; one wants to believe it. Theoretically there could be just such differences in racial characters. If they exist, they could constitute a control of culture by inherent biological characteristics, so long as the differing peoples do not communicate with one another. Doubtless civilized and savage peoples are such partly because of genetic differences, but it would be interesting to see what would happen if they intermingled freely without interbreeding. Whether two more or less civilized peoples differ in their capacity to create—not just absorb—certain types of culture is a question which is likely to wait a long time for a sure answer.

Man in the Americas. The Western Hemisphere has furnished none of the evidence of the origin of man. The oldest bones yet found, if conclusions from studies are to be taken at face value, are those near Mexico City (Tepexpan man, Fig. 59), dating from about 11,000 years ago. The dating was done partly by means of radioactive carbon, whose half life is about 5570 years, as an average of a number of tests. A mammoth and an aquatic bird were also discovered there. The man was about 5 feet 7 inches tall, his cranial capacity about 1540 cc. From the bones the blood group is tentatively determined as A, unlike most American Indians of today (group O). Artifacts of preceramic type were found with the bones.

The next oldest fossils on which there is general agreement are probably no more—most likely less—than 5000 years old. They were in two caves in Patagonia. They were on the rock floors of the caves, with debris of four cultures above them, so they must have been the first in that area. They were modern human beings, similar to the American Indians. Several skeletons have been found in Minnesota, and for one of them an age of 20,000 years is claimed by one anthropologist, while another considers it a typical Sioux Indian like those still alive. The age of the deposits is hard to determine in most such cases.

It seems certain, then, that the primate stock that gave rise to man did not live in the New World. South America has its primates, but the great apes are all oriental. They and Pithecanthropus were geographically placed so that they could have come from the same ancestry.

Until the year 1926 it was generally held that the Shell Mound peo-

ple of the western coast and the Basket Makers of the Southwest were the earliest men in North America, and they need not be more than three thousand years old. In that year, however, a couple of stone points, probably the heads of lances, were found at Folsom, New
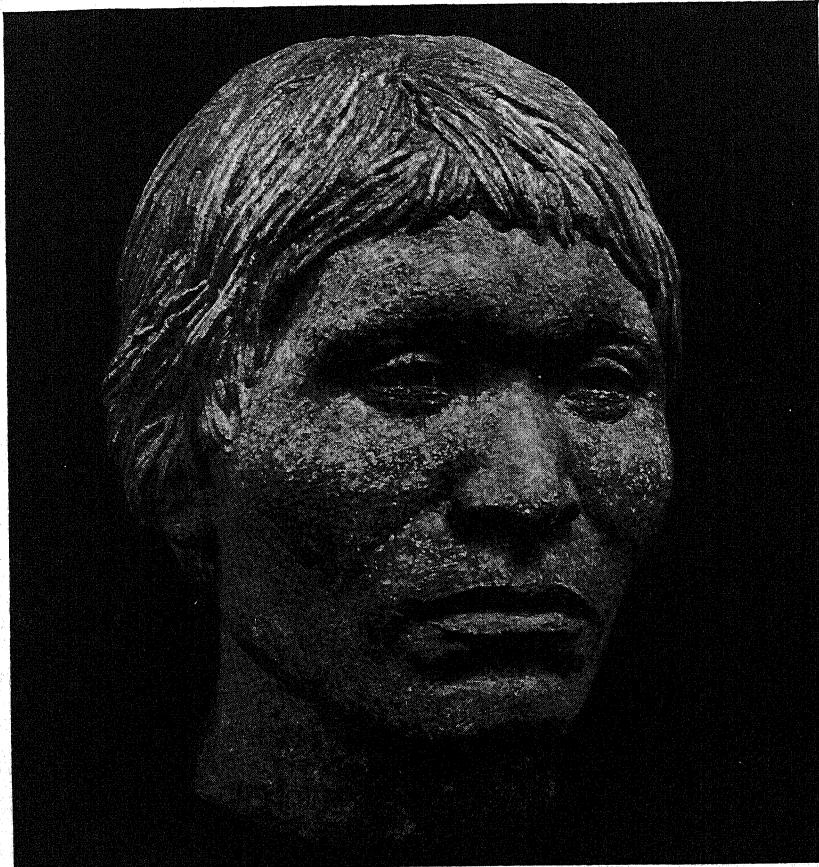
FIG. 59. Tepexpan man, from reconstruction by Leo Steppat. (*From DeTerra, Romero, and Stewart, Tepexpan Man, courtesy of Viking Fund.*)

Mexico, associated with bones of a bison. This animal was not the modern bison but of an extinct species that had been dated back to the end of the Ice Age, which should be roughly 25,000 years ago. Other such points, again associated with the bison bones, were discovered later and were examined in place by anthropologists. Some 23 bison were eventually found there, as if they had been rounded

up and slaughtered at that very place. More of the stone points were with them. Not all anthropologists set the time as long ago as the Ice Age, but even the 15,000 years the others accept is much older than any human bones ever found in America. Radioactive-carbon tests of the age of woody materials closely associated with the Folsom points and the bison are not yet available. Thus we know early American man's culture slightly but American man himself scarcely at all.

Other points like those at Folsom have been found in Nebraska (with extinct elephant bones), in Colorado (also with a mammoth), and at other places in New Mexico besides Folsom. Near Carlsbad a point was buried *under* the Basket Maker culture, with bones somewhat like those of a musk ox, indicating perhaps a cold climate, since the musk ox is now an arctic beast. No signs of art have been found, which makes American men look more primitive than their European contemporaries—but negative evidence always has a chance of being refuted by a positive find.

The American Indians and Eskimos are all Mongoloids, and it is assumed they came from Asia. The two continents have been more or less connected at intervals, and even now are within sight of one another across Bering Strait, so that boats could carry adventurous human beings across. Support for the theory that Bering Strait was actually crossed is the discovery, in Alaska next to the strait, of tools like some that were used in the Old World up to about 4000 B.C. and 8000 B.C., respectively. The characteristics of the Eskimo and American Indian types are nearest to those of the Tibetans in Asia, so that may have been their source. In the Western Hemisphere they have wandered all the way to the tip of South America. They were hunters and trappers, but were also food producers. They grew corn, potatoes, tomatoes, and squash which their white European "discoverers" had never eaten, and tobacco which Europeans had never smoked. Yet at only three places did they develop civilizations: the Aztecs in Mexico, the Mayas in Yucatán and Guatemala, and the Incas in the Andes of Peru.

MECHANISM OF PERMANENCE AND CHANGE

> The germ cells are the only living bonds not only between generations but also between species, and they contain the physical basis not only of heredity but also of evolution.
>
> —E. G. CONKLIN, 1934

The most important thing to know about a natural phenomenon is the reason for it. What are the steps by which it occurred, how did one lead to another, and what started them in the first place? It is worth while to know the causes even if the time and energy spent in ascertaining them prevent the acquisition of some additional observable cold facts. The advantage of knowing causes lies in the insight it gives into situations not open to easy observation, and the ability to forecast what could or could not be expected in fields where observations seem equivocal. The greater part of the remainder of this book is devoted to laying bare the processes which must have brought about the evolution whose existence is so amply demonstrated in the preceding chapters.

Evolution may be pictured as a series of changes which are more or less permanent—continuing, that is, until other changes replace them. The permanence that organisms enjoy is vouchsafed them by heredity. A philosopher knowing nothing about the constitution of living things might well feel justified in postulating that evolution consists either (1) of changes that are produced and then are made hereditary, or (2) of alterations in things that are already inherited. The first of these postulates meets an obstacle in the fact that higher animals and plants have no machinery whereby ordinary changes in their body make-up could be made permanent. There is, moreover, much evidence from experiment that modifications of the body of an organism are not inherited. The second possibility, however, has a biological basis. The things which control heredity are well known, and it has been repeatedly shown that they may be altered. Besides,

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the phenomenon of heredity itself involves change as part of its reg-
ular manifestation.

The study of evolution is thus simplified by the circumstance that
both it and heredity rest on the same physical basis. The mechanism
of heredity is also the mechanism of evolution. The genetic mechanism
is responsible for both permanence and change. Let us see what that
mechanism is.

Chromosomes and Genes. The readily visible, though microscopic,
parts of the evolution (and heredity) mechanism are the *chromo-
somes*, highly stainable objects residing in the nuclei of most kinds of
cells. In the chromosomes are the ultimate units of permanence (and
change), the *genes*. Genes are not visible, and chromosomes can usu-
ally be separately seen only at the time of cell division. Since that di-
vision involves some other things of significance in evolution, it should
be understood.

In the nucleus of a cell the chromosomes exist in such fine thread-
like form that they are not seen as distinct bodies. Early in cell division,
however, they shorten by coiling into close spirals, which gives them
an apparent thickness that they really do not possess. Each chromo-
some includes, somewhere in its length, a *centromere*, which is re-
sponsible for its movements during division. By their centromeres, the
chromosomes are moved into a flat group, circular in form if there
are many chromosomes. The plane of this group lies across the middle
of a spindle, consisting to all appearances of fibers, which has been
forming while the chromosomes have been condensing. These features
are mostly shown in Fig. 60, which is simplified by having only six
chromosomes. Most cells contain a much larger number. The shapes
of elongated chromosomes are determined by the position of the cen-
tromere, which is sometimes at the end, sometimes in the middle, some-
times off center. As the centromeres move, the chromosomes trail
along, becoming rod-shaped, V-shaped or J-shaped, as in the figure.

Before the chromosomes move into the middle plane of the spindle,
each one is transformed into two identical chromosomes. In general
biology, this process is usually called division of the chromosomes,
and for some parts of the material of the chromosomes that word is
probably satisfactory. For the genes in the chromosomes, for reasons
that will be clear later, duplication is a better term. Almost certainly
genes do not divide, but it is highly characteristic of them that they
duplicate themselves.

The centromeres do not participate in the early duplication of the
chromosomes; they remain single until after the doubled chromo-
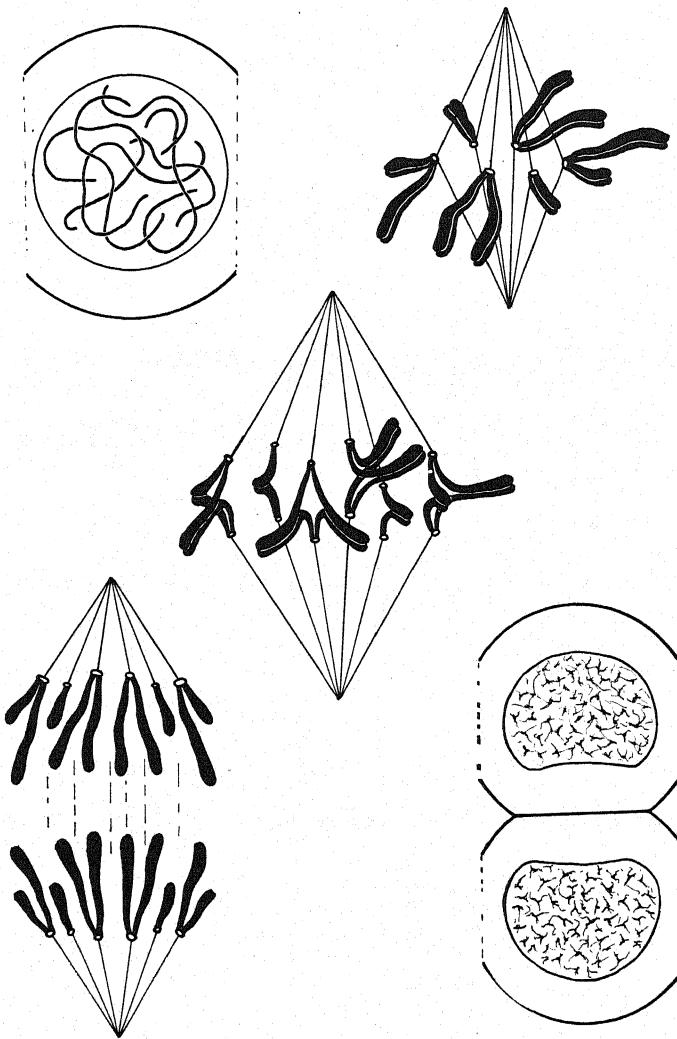
FIG. 60. Mitotic cell division. In the *upper right* and *central* figures, the upper end of the spindle is tilted toward the observer.

somes are arranged in the middle of the spindle. Then the centromeres divide quickly, and their parts move rapidly toward opposite ends of the spindle, each pulling one of the duplicate chromosomes with it. At the ends of the spindle, the chromosomes uncoil from their condensing spirals, to form the slender threads of an ordinary nucleus. The body of the cell then divides between these new nuclei, and two

identical cells replace the one from which they came. In particular, the genes of one of these cells are exactly like those of the other, and exactly like the genes of the cell which divided.

This is the kind of division by which a fertilized egg produces the millions of cells of the body of an animal or plant. Accordingly, all these cells should contain identical genes. Cytologists have sometimes thought divisions were less regular than the one here portrayed, and in certain situations the genes change, though not necessarily at the time of cell division. Yet in general the prevailing view is still that body cells are genetically all alike.

Meiosis. In the production of germ cells, on the contrary, there is a mechanism which makes the mature germ cells of many different kinds. One cell division in their maturation inevitably makes them dif-
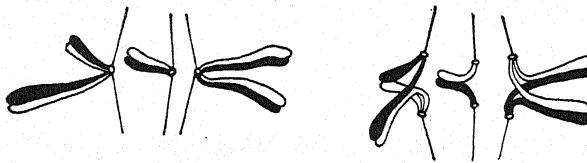
FIG. 61. Meiosis, with maternal and paternal chromosomes distinguished.

ferent for most organisms. Indeed, in an evolutionary sense, making the germ cells different is the particular function of that division. The bulk of evolution in the end depends on that differentiating kind of cell division.

To understand this division, one must remember that in bisexual animals half the chromosomes in a body cell have come from the father, the other half from the mother. The paternal chromosomes are similar, in shape and gene content, to the maternal ones. In Fig. 60, one of the J-shaped chromosomes is paternal, the other maternal. Similarly the two rod-shaped chromosomes came from different parents. All the chromosomes, with certain exceptions related to sex, exist in pairs from the two parental sources.

When reproductive cells are ready to undergo their transformation into mature germ cells, the homologous chromosomes come together in pairs. There is some sort of attraction between homologous genes at this stage, as a result of which the similar chromosomes join side by side. In one of the two divisions which follow, these pairs of chromosomes are placed on the middle plane of the spindle, with the maternal chromosome facing one end, the paternal chromosome the other end, of the spindle. Then the chromosomes are pulled apart by

the movement of their respective centromeres (Fig. 61). At each end of the spindle there are assembled only half the complement of chromosomes—three in place of six in the illustration. From this reduction in number of chromosomes, the division was first called the reduction division. The common name for it now is *meiosis*. The essential feature of it is separation of homologous maternal and paternal chromosomes, and genes, into different cells.

In this division, as described, no chromosome has been duplicated; whole chromosomes have parted company. The facts are not quite as stated, but to avoid complexities that do not particularly concern evolution, we may allow the description to stand for the present. Another division follows, in which chromosomes *are* duplicated, just as in division of body cells. The final germ cells have the reduced, or *haploid*, number of chromosomes, as contrasted with the *diploid* number which
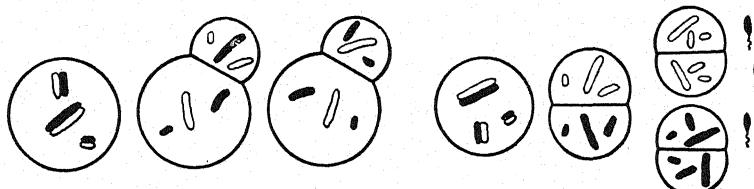
Fig. 62. Meiosis in animals; female cells, *left*, male cells, *right*.

body cells and early reproductive cells have. The two divisions in animals are represented in condensed form in Fig. 62. The female cells, at the left, divide very unequally. The small cells, known as *polar bodies*, are not functional, and the two divisions result in only one egg. The male cells, at the right, divide equally, and four spermatozoa are formed from one initial cell. In this figure the first division shows whole chromosomes being parted (meiosis); the second division has them duplicated. Actually, each division separates some paternal *genes* from the corresponding maternal ones. Both divisions are in this sense meiotic, and they are distinguished as first and second meiotic divisions. This feature is referred to more particularly in a later section.

Meiosis in Flowering Plants. The separation of homologous chromosomes and genes into different cells in flowering plants occurs slightly earlier than in animals. Production of an egg is initiated by a large cell centrally located in the female part of the flower. When this cell divides, the separation of maternal and paternal chromosomes occurs. Following this is another division in which chromosomes are duplicated. Four cells, all haploid, result, but only one functions (Fig. 63).

This cell divides three times, producing an eight-cell *embryo sac*. Three of the eight cells go to one end of the embryo sac and ultimately degenerate. Three others go to the other end, and the middle one of these is the egg. The remaining two of the eight go to the middle and contribute to the *endosperm*, or nutritive tissue, of the seed. All eight cells are haploid.

Pollen develops in the anthers. Numerous cells there divide twice, the first time by meiosis. Each of the four haploid cells thus produced, in forming one pollen grain, divides once unequally. The larger cell is called the *pollen-tube cell*. When the pollen falls on the stigma of a
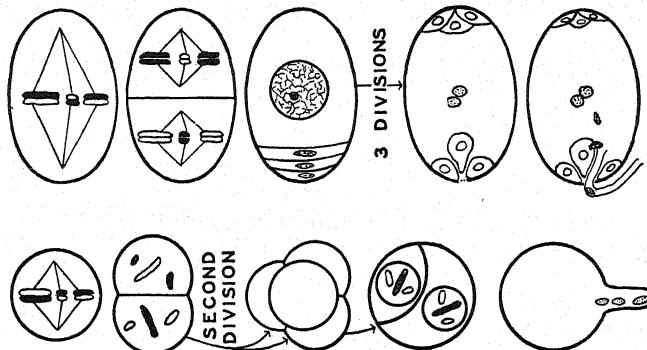
FIG. 63. Meiosis in flowering plants, female, *above*, male, *below*. In germinating pollen, *lower right*, nucleus at tip of growing tube is pollen-tube nucleus; the two at *left* of it are the sperm.

flower, it develops a tube which grows down through the style of the flower. The pollen-tube nucleus leads the way down the tube and is regarded as governing the tube's growth. The small cell of the pollen grain divides into two *sperm* (Fig. 63) as the tube grows, and these follow down the tube behind the tube nucleus. The tube enters an embryo sac, where it bursts open, liberating the two sperm, while the tube nucleus remains behind and degenerates. One sperm fertilizes the egg; the other sperm joins the two nuclei at the center to help produce the endosperm (upper right, Fig. 63). The endosperm is therefore *triploid;* it has half again as many chromosomes as the fertilized egg.

Recombination of Chromosomes. From the standpoint of evolution, the important feature of meiosis is that the pairs of chromosomes are placed at random on the spindle. Either maternal or paternal chromosome may face a given end of the spindle. The position taken by one pair does not influence in any way the position of the other pairs. In

Fig. 61 the J-shaped pair at the left is turned one way, the other two pairs the opposite way. This arrangement is one of eight into which three pairs of chromosomes may enter. Other arrangements are shown in Figs. 62 and 63. The chromosomes turned toward the same end of the spindle are the ones which enter one germ cell, so there are eight kinds of germ cells when there are three pairs of chromosomes.

The number of kinds of germ cells increases rapidly as the number of chromosomes grows. Each added pair of chromosomes doubles the number of kinds of germ cells. Man, with his 24 pairs of chromosomes, produces 2^{24} different combinations of maternal and paternal chromosomes in his germ cells.

Crossing Over. If chromosomes remained intact, forever of the same constitution, the combinations of maternal and paternal chromosomes would be the limit of possible variation in the germ cells. They do not, however, remain intact. A long chromosome probably breaks at one or more places in every meiosis. It comes out of meiosis looking just as it did before. If it was large before, it is large afterward. If it was J-shaped before, it is J-shaped after meiosis. The centromere is still at the same point in its length. Its gross appearance is unchanged because any breakage in it results in an even exchange. Another chromosome breaks at the same time, at the same place, and in the exchange each chromosome receives as much as it relinquishes. This exchange is known as *crossing over.*

To illustrate what happens in crossing over, a single chromosome pair will suffice. Let us use the J-shaped chromosome at the left in Fig. 61. One feature of such a pair has not been shown in the diagram. As the chromosomes come together side by side, each one has become duplicated—in preparation for one of the two divisions. The pair thus becomes a four-strand structure, two of the four parts paternal, the other two maternal. Such a *tetrad,* as it is called, is diagrammatically represented at the top, left, of Fig. 64.

The exchange referred to may occur between either of the paternal strands (*chromatids*) and either of the maternals. Apparently there is no exchange between the two paternal chromatids, nor between the two maternals; anyway, such an exchange would have no evolutionary significance because the two sister chromatids are exactly alike. One of the maternal chromatids may even exchange parts with both of the paternals but at different places in their length; and a paternal may exchange with both maternals at different levels; or both may exchange with both. Indeed, such triangular or quadrilateral trades are common. As a result of such shifts, one part of a maternal chromatid may

be separated from the corresponding part of the paternal in the first division, while another part of the maternal is separated from the paternal in the second division. This is an excellent reason for calling both divisions meiosis.

These facts are of some importance in genetics and are here recorded because they are facts. They are not, however, particularly significant in evolution. The essential feature of crossing over can be illustrated
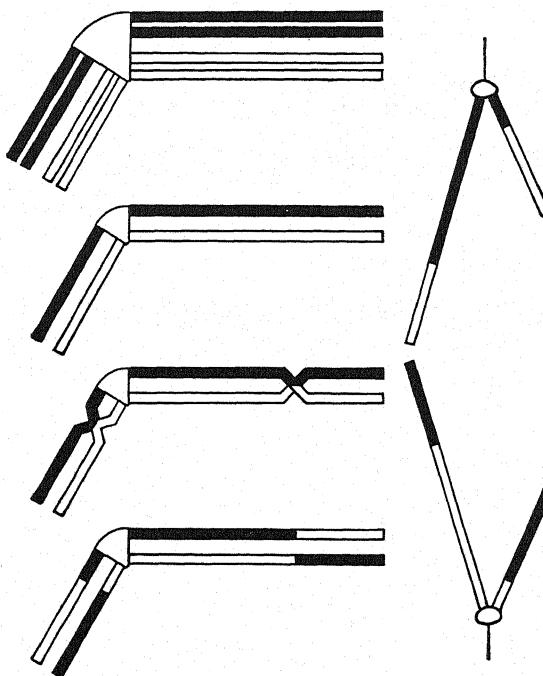
FIG. 64. Diagram of crossing over in meiosis. *Top,* tetrad. Other figures simplified by omitting one maternal and one paternal chromatid.

with only two chromatids, one paternal and one maternal. We accordingly dispense with half the tetrad in the remainder of Fig. 64.

At some early stage the homologues may become attached at one or more points, perhaps in some way connected with their viscosity, though the reason is not understood. A crosslike connection between the chromosomes is thus formed (Fig. 64). Usually, though probably not always, when the chromosomes finally separate, each comes away with part of the other. The parts exchanged are equivalent, for the point of breakage is the same in both. That is, if the paternal chromo-

some breaks between neighboring genes *b* and *w*, the maternal one also breaks between genes *b* and *w*—or between *b* and *W*, or *B* and *W*, if the genes are slightly different in the two chromosomes. Since the genes beyond the break are homologous in the two chromosomes, the exchange is an even one.

Recombination of Genes. Crossing over (the breakage) may occur at any point in the length of the chromosomes, that is, between any two genes. There is evidence in some of the genetically best-known organisms that some parts experience crossing over more frequently than other parts of the same chromosomes. In one of these, the greater frequencies are far from the centromere. But there is no evidence that any part is immune. Every gene can be separated from its nearest neighbors. If there are two or three crossovers at each meiosis, on the average, and the chromosomes have a thousand genes, it would take quite a number of generations to effect every one of the possible separations. However, evolution is a long-time process; it has any number of generations at its disposal.

Because of crossing over, the unit of recombination at meiosis is no longer the chromosome; it is the gene. How long two genes must wait to be separated by crossing over influences the results of a genetic experiment, which lasts only two or three generations, but not evolution, which extends over thousands of generations. This is because, once a rare crossover occurs, the newly neighboring genes remain neighbors as tenaciously as they previously avoided one another. After a number of generations which must seem very moderate in natural evolution, it is quite impossible to detect differences in the frequencies of combinations of genes in chromosomes resulting from very close linkages of some of them. Under these circumstances, the genes really are the units of recombination.

It is too soon to use this fact to make computations of the possible number of gene combinations, as was earlier done for combinations of maternal and paternal chromosomes. The number of chromosome combinations, as we have seen, is 2^n, in which n is the number of pairs of chromosomes. For the genes, the basic number is seldom 2, and its exponent is different for different kinds of animals and for different strains within the same species. What the substitutes for 2 and n are is determined by phenomena described in the next chapter. These phenomena are really part of the mechanism of change and could properly be included with mitosis and meiosis in one account. They are, however, of irregular occurrence, not inherent in the generation-to-generation workings of heredity, and are for this reason treated separately.

PRIMARY VARIATION

The basic change factor is gene mutation, the occasional failure of precise duplication. . . . It only requires a very moderate mutation rate in a large population for the number of unfixed loci to become enormous.

—SEWALL WRIGHT, 1931

There is thus solid foundation for the attempt which has been made in the past twenty years to analyse evolution by reference to laboratory experiments on mutation and structural rearrangement.

—M. J. D. WHITE, 1948

The chromosome mechanism described in the preceding chapter is only the gross framework on which the detailed operation of both heredity and evolution rest. Some of the details must now be added. A chromosome consists of a protein skeleton to which the genes are attached, or it is a protein organization of which the genes are a part. While the chromosomal proteins in general have functions related to control, the specific nature of development and physiological processes is determined by the genes. These genes are arranged along the length of the chromosomes in a pattern which shows considerable persistence. Because of this persistence, the chromosomes possess an individuality which tends to continue through indefinite numbers of generations. Continuity of chromosome pattern and identity of genes depend on processes of reproduction. Chromosome reproduction leads to new chromosomes that are at least very similar to their predecessors, and reproduction of genes is highly specific. Yet even the genes are not always faithfully duplicated in reproduction.

Changes of genes are called mutations; changes of chromosomes are given various names such as aberrations, structural rearrangement, or reorganization. As we shall see, to distinguish mutations of genes from structural rearrangement of chromosomes is easier on paper than it is

in practice, but in the following account we shall attempt to make that distinction.

Mutation. To understand the changes to which genes are occasionally subject, it is necessary to know their structure and their mode of reproduction. A gene is almost certainly a protein molecule. Proteins are made up of amino acids, of which there are some twenty different kinds, linked to one another by peptide bonds. Fundamentally the molecule is a long chain, but in functional situations this chain may be folded on itself many times. The size of the molecule may be judged partly from its molecular weight, as compared with the molecular
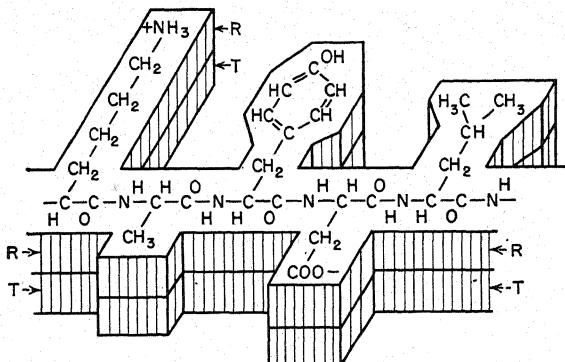
FIG. 65. Reproduction of a peptide chain, in which the amino acids are lysine, alanine, tyrosine, aspartic acid, and leucine. *T*, template; *R*, replica. (*From Haurowitz in Quarterly Review of Biology, The Williams & Wilkins Company.*)

weights of the amino acids. A globulin, for example, would have to include about 1500 amino acid molecules to make up its molecular weight of, say, 175,000. A peptide chain made up of 1500 amino acid molecules would be about 0.5 micron in length. (A micron is one-thousandth of a millimeter.) A stained filament of that length could be seen in a microscope except for its slenderness. Incidentally one may point out the tremendous variability which such molecules may possess. If each of the 20 amino acids may occupy any or all of the 1500 positions in the chain, there are 20^{1500} conceivable kinds of molecule. If evolution were to depend on variations in such molecules, it could go on a long time before its possibilities were exhausted.

The nature of gene reproduction is largely speculative, but it has been suggested by more than one biochemist that the chain must be in extended form in order to expose all parts of it to the supply of amino acids, etc., of which a new molecule would have to be constructed.

The old molecule acts as a template, or model, in relation to which the replica is laid down (Fig. 65). Adsorption of like components— leucine by leucyl residue, alanine by alanyl residue—could be part of the copying process, though it is not clear just why there should be such correspondence in adsorption. Whatever the explanation may be, there *is* just such an exact duplication of the genes at every chromosome duplication.

So complex a process could hardly be expected to be repeated always without a slip. It would be hazardous to suggest what the nature of any errors might be, but it requires little imagination to picture the replacement of one amino acid with another in one of the 1500 positions, or exchange of positions by neighboring amino acids, or some less radical change within these components of the molecule. Almost any change which the structure of the molecule permits would alter the influence of the gene on development, and some characteristic of the organism harboring an altered pair of genes would be changed. While the details of mutation here pictured could easily be wrong, the more or less permanent change of some characteristic which is then inherited in accord with the usual rules of heredity is proof that a gene has mutated. Discovery of mutations always comes from the detection of changed inherited characteristics.

Examples of Mutations. Selecting specific changes as examples of mutations forces the admission, hinted at earlier, that it is usually
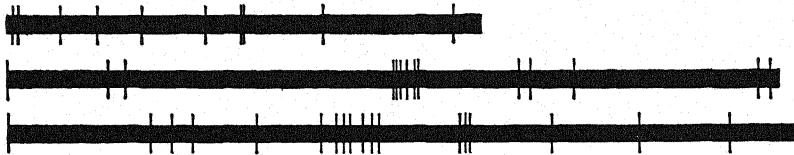
FIG. 66. Position of 42 genes in the three principal chromosomes of Drosophila that affect eye color. Omitted are a few that merely modify the action of other eye-color genes. No genes of the minute fourth chromosome are known to influence eye color.

impossible to say with assurance that a given inherited change is caused by mutation of a gene, and not by structural rearrangement within a chromosome. It is usually assumed that the less radical changes are gene mutations. Also, when a changed type can revert to its original form, the change is assumed to be a mutation, though the number that have so reverted is too small to be very useful. When a change is not accompanied by visible changes in the chromosomes,

in situations where the chromosomes could reveal a reorganization, the belief that a gene has mutated is strengthened.

The vinegar fly Drosophila has revealed many changes, and geneticists have mostly assumed that the recessive visible ones among these are real mutations of genes. The eye color, normally a red (whose quality is dependent on two pigments, a red and a brown), has changed to brown, claret, scarlet, vermilion, ruby, white, and others. Each of the colors named results from mutation of a different gene.
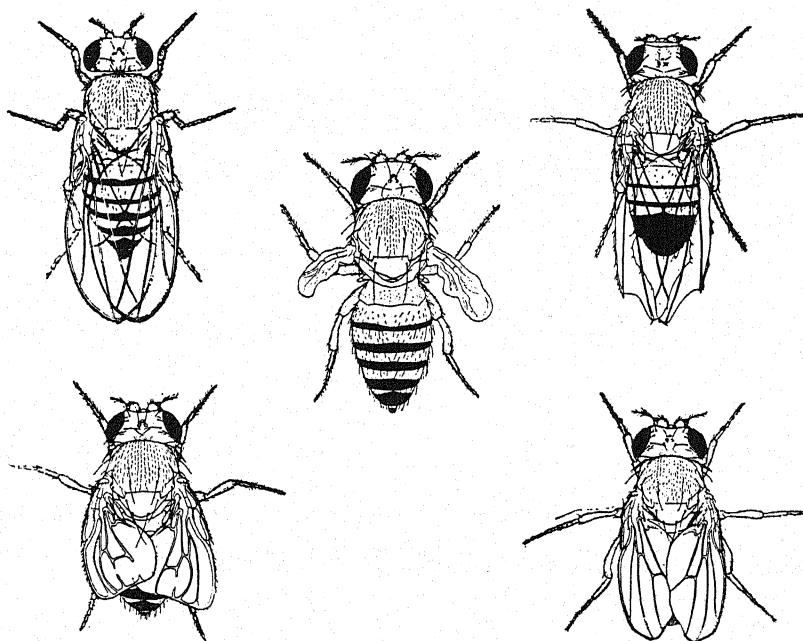
Fig. 67. Various wing mutations in Drosophila. Wild-type wing for comparison, *upper left*. Others are cut, vestigial, rudimentary, and miniature. (*Drawings by E. M. Wallace, from Sturtevant and Beadle, Introduction to Genetics, W. B. Saunders Company.*)

There are at least 42 genes in Drosophila, scattered along all the chromosomes except the small fourth one (Fig. 66), whose mutations change eye color. They effect the change by altering the amount of either the red or the brown pigment or both. Some of the end products are so much alike, for example, vermilion and scarlet, that they cannot be distinguished by appearance, but they are inherited differently. The bristles of this fly are changed in shape; the body color, normally a grayish brown, may become black, tan, or yellow; the wings

EVOLUTION

are shortened or made irregular in form (Fig. 67); the ocelli on top of
the head are whitened; the balancers (vestiges of a second pair of
wings) are expanded into more winglike form; the tarsi lose one joint;
the reaction to light is changed; tumorlike growths are induced; hatch-
ing is hindered; viability is diminished—every part of the organization
has been modified in one or more ways.

Mice have produced new coat colors, eye colors, tail shapes, and
spots; guinea pigs have produced long hair; poultry have changed
combs and plumage; corn originates new grain colors, cob colors, and
numbers of rows of grains per ear; the bacterium *Escherichia coli* has
had its resistance to bacteriophage altered; every plant or animal that
has been extensively bred under careful observation, especially if
changes are being looked for, has revealed mutations. Fairly well-
established mutations in man are on record—to albinism, to congenital
baldness, to the disease alkaptonuria, repeatedly to hemophilia and
several other defects—though the proof that the character had not
been present in the ancestry is seldom as rigid as for the laboratory
animals and plants. There is every reason to suppose not only that
every organism is subject to such change, but that every gene is ca-
pable of mutation. Current evolution theory is based on that assump-
tion.

Structural Changes in Chromosomes. To produce a change in the
characteristic pattern of genes in a chromosome, the chromosome must

FIG. 68. Three successive inversions
in one chromosome. Curved arrows
indicate rotation of segment
through 180 degrees. Final chromo-
some, *bottom*, has only four of its
nine genes in their original position.

break. The breakage occurs between
genes. If there is an internode of non-
genic material between the genes, the
break occurs in that internode; if
the genes adjoin one another without
intervening material, the break is a
clean-cut separation of them. In the
latter case, it would seem possible that
separation might occasionally cause
mutation in one or both of the genes
separated, and some geneticists have
listed chromosome breakages as one
of the possible sources of mutation,
but such a result could hardly be
proved. Breakage of chromosomes pre-

sumably occurs only in their threadlike form, not in the condensed
spiral, and would be the result of some unusual tension. Such tension
could be produced as a rare concatenation of normal physiological

conditions, just as 20 tossed coins *could* occasionally turn all heads up. Probably only one break could occur at a time if done in this way. Temperature shock or a sudden abnormal physiological condition could break two or more chromosomes or one chromosome at more than one place at the same time. What happens afterwards depends on the number of breakages.

When a chromosome breaks, there is a strong tendency for a broken end to join only with another broken end, though there is evidence that a broken end *may* join with the natural end of a chromosome. If there is only one break, the raw ends usually rejoin, since there is little
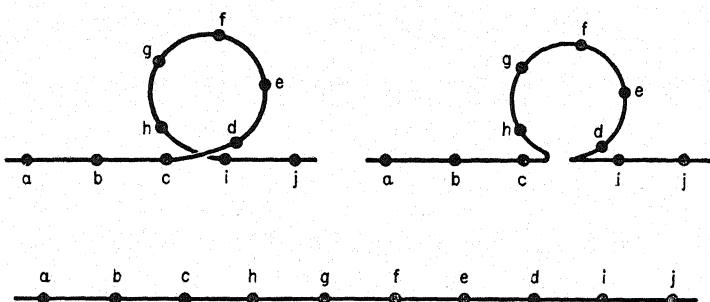
FIG. 69. Inversion aided by a loop. If breaks occur near place where chromosome crosses itself, broken ends are near enough together to make exchange in rejoining.

else for them to do. Such a break is not detected, because it leaves the chromosome unchanged. If there are two breakages, with four broken ends, the raw ends may join in new ways. If the two breakages are in the same chromosome, the segment between them may simply turn through half a circle and join the opposite end segments of the chromosome (Fig. 68). Such a change is called an *inversion*. This kind of reorganization would be more likely to happen if the chromosome were coiled in a loop, so that the four broken ends were near one another (Fig. 69). If a second inversion occurs within the first one, the result is that shown in the third chromosome of Fig. 68. A further inversion, this time overlapping the first two, would produce the bottom chromosome of that figure.

If two breaks occur simultaneously in nonhomologous chromosomes, as in the upper left of Fig. 70, there may be an exchange of segments between them, producing the two to the right of them. This exchange is known as *translocation*. If there are two breakages in one chromosome, one in another (lower left), the released internal segment of the

first may be inserted at the break of the second (two at lower right of Fig. 70). This is also translocation, but is not an exchange.

Finally, if one chromosome breaks at two points, particularly if the two are not far apart, and its homologue breaks at one point which is at the same level as one of the breaks in the first chromosome, a small segment of the first chromosome may be inserted in the second (Fig. 71). This produces what is called a *repeat*. In the figure, the segment containing genes B and C is followed by another exactly like it in the lower right chromosome. This change can also be called a *duplication,* but the latter name is applied to the occurrence of any gene or
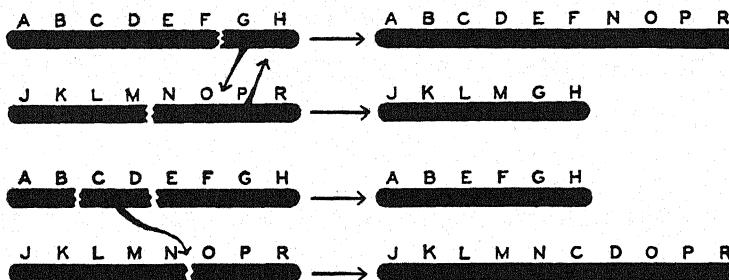
FIG. 70. Translocation, or transfer of part of a chromosome to a nonhomologous chromosome. Upper half constitutes *reciprocal* translocation.

genes more than the usual two times (in a diploid organism) in the same cell. Translocation could eventually result in duplication in this sense. Repeats are successive segments in the same chromosome, each containing the same genes in the same pattern.

The repeat just described leaves one chromosome without certain of its genes. That lack is known as a *deletion* or *deficiency*. Following divisions may result in cells that possess such a deletion in one chromosome of a pair; having it in both chromosomes is usually fatal unless the same genes have been carried elsewhere in the chromosome group by translocation.

These several types of chromosome breakage will serve to illustrate what may happen in the reorganization of the evolution mechanism. Such changes happen in nature, and later on some examples of their natural occurrence will be given. For the present the methods of producing them must suffice.

Effect of Repeats. It might be supposed that a considerable part of the reorganization of chromosome structure would mean nothing in

evolution. Many of the changes illustrated would leave the cell possessed of exactly the same genes—none added, none lost. Some of the changes leave the kinds of genes the same, but a larger number of some of them in the same cell. Repeats are, and translocations may be, of this kind. Such additions have an effect on the nature of the organism.

A classical instance of this effect is that of bar eye in Drosophila (Fig. 72). Bar eye is an irregular band in which the number of simple units, or ommatidia, is greatly reduced. Our knowledge of the nature of bar eye comes from the fortunate circumstance that in the salivary glands of the larvae of these flies the chromosomes are enormously enlarged. The chromosomes are also marked with numerous stainable crossbands which either are, or contain, the genes. The bands are of
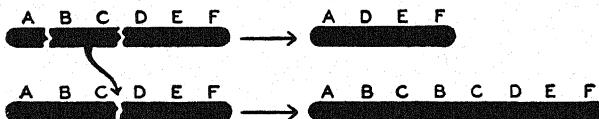
Fig. 71. Repetition of same genes (*BC*) in successive segments of same chromosome, through breakage and transfer.

different structure and different staining properties, so that they have been recognized as forming a definite and persistent pattern running through the whole group of chromosomes.

Bar eye is not a mutation at all, in the strict sense of a changed gene adopted for this book; it is instead a repeat. Five bands of the salivary-gland chromosomes are involved in this repeat. The wild-type fly has all five of these bands; bar-eyed flies have the same five bands twice (Fig. 73). Having these five bands once in each chromosome of the pair (wild type) gives the eye some 779 ommatidia on the average. Having the five bands once in one chromosome, and twice in the other (heterozygous bar) reduces the number of ommatidia to about 358. Having the five bands twice in both chromosomes (homozygous bar) reduces the ommatidia still further to 68. By an unequal crossing over in which the break of one chromosome comes between the two groups of five bands, and that of the other chromosome at one limit of the repeats, a bar chromosome may revert to a wild-type chromosome having the five bands only once. The same kind of unequal crossing over may yield a chromosome which has the five bands three times (double bar, Fig. 73). A fly heterozygous for this condition, that is, having the five bands three times in one chromosome, only

once in the other, has about 45 ommatidia. If it is homozygous, having the five bands three times in each chromosome, the ommatidia are reduced to 25. A further increase in the number of groups of five bands has been reported but without further reduction in the number of ommatidia.

Hairy wing is another Drosophila character that springs from repetition of the same genes rather than from a mutation. In organisms not
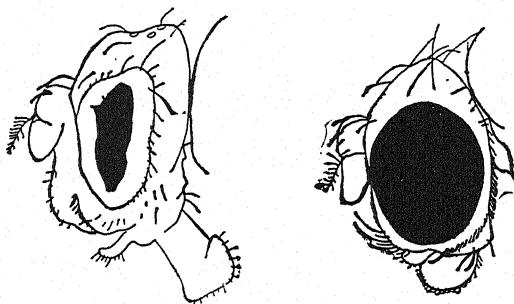
FIG. 72. Bar eye and normal eye in Drosophila. (*From Morgan et al., Mechanism of Mendelian Heredity, Henry Holt and Company, Inc.*)

provided with banded chromosomes it is not easy to detect such tandem repetitions.

Position Effect. Bar eye in Drosophila (see above) also illustrates the effect of shifting genes to another place in the chromosomes. Homozygous bar, having four groups of the five bands, two groups in each chromosome, has about 68 ommatidia. Heterozygous double bar also has four groups of the five bands, but three of them are in one chromosome, one in the other. This kind of fly has on the average only 45 ommatidia. Exactly the same genes are present in both homozygous bar and heterozygous double bar. But their eyes are not alike. The four groups of bands (genes) reduce the eye more if they are divided three and one between the chromosomes than if they are divided two and two.

Certain mild imitations of bar eye turn out to be position effects involving one of the bands in the five-band repeated region already described. Some inversions and translocations which involved breaks in this region, and which carried part of that region to other places in the chromosomes, produced a barlike effect on the eye. The crucial point of breakage seems to be next to the first heavy crossband in section 16A (see Fig. 73 for this location). Placing this or the adjoin-

ing band in close relation with some strange gene or genes may be the reason for the reduction in the number of ommatidia.

Lozenge eye in Drosophila is also caused by three identical and successive segments of the chromosome. It also shows a position effect. If all three lozenge segments are in one chromosome and only the wild-type arrangement in the other, the fly is wild type. But if pre-
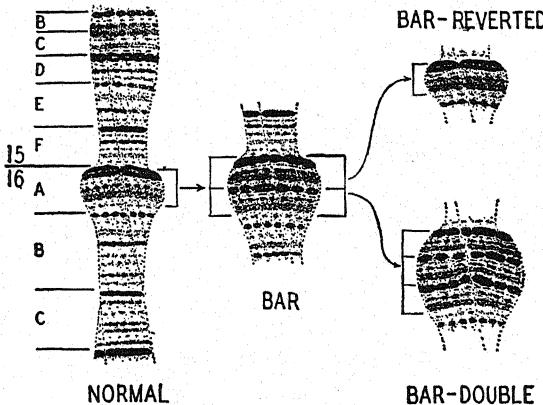
FIG. 73. The repeated bands, involving repeated genes, in the salivary-gland chromosomes of bar-eyed Drosophila. (*From Bridges in Science.*)

cisely the same added lozenge segments are divided between the chromosomes, the eye is lozenge.

Other position effects in Drosophila have been the weakening of dominance of genes displaced by translocation or inversion. The wild-type genes were no longer quite dominant over the genes for yellow body and forked bristles when they were moved to other places in the chromosome by inversion. The gene for an interrupted cubitus vein of the wings, which is normally recessive, nevertheless shows some of this interruption of the vein in a heterozygote if the wild-type gene is translocated to another chromosome.

Out of a number of such position effects in Drosophila has come the revelation that the influence of a strange gene may extend farther than just to the adjoining genes. The influence may go as far as a dozen bands in the salivary-gland chromosomes.

Most of the information about position effects come from Drosophila. Partly this is because, with its chromosome bands in the salivary glands, it shows what the changes of position actually are. How important this effect is in evolution is uncertain. In corn, where

chromosome reorganization can also be produced, and detected cytologically, position effect is unknown.

X Rays a Mutagenic Agent. In seeking the agencies responsible for the primary variation on which evolution rests, it is necessary to throw together the mutations and chromosome aberrations, because they often cannot be distinguished. Only in organisms having a visibly identifiable chromosome pattern, as in the salivary glands of Drosophila, is it possible to say with assurance precisely what has been done to the chromosomes. When a genetic character is changed, and no alteration of these chromosomes can be detected, it still is not certain that the alteration is a mutation, for very small inversions or translocations would perhaps not be seen. Accordingly, in considering the causes of change we shall be concerned with any primary modifications which might lead to evolution.

Of the known agencies producing genetic alterations, most are environmental; a few are within the organisms. Radiation has been the greatest source of artificially produced mutations and chromosome breakages. X rays have produced such changes in many different kinds of plants and animals. They are most effective at certain stages of the chromosome cycle; in the fly Sciara, for example, the chromosomes are immune to 1100 r units until the nuclear membrane dissolves in the first meiotic division. After that, this dosage applied in prophase yields 5 per cent of oöcytes with some kind of chromosome reorganization, in metaphase 28 per cent, and in early, middle, and late anaphases, 30, 50, and 40 per cent, respectively. Germ cells must be reached directly by the rays; when the gonads are protected by appropriate shields, there is no increase in mutation. Within a certain range, the effect of X rays is proportional to dosage; doubling the dosage doubles the number of mutations. It has generally been held that chromosome breakage was produced when a sensitive spot in the chromosome was directly hit by an ionizing particle, hence that such changes occur only while irradiation is taking place. Some experimenters have held, however, that there must be at least some delayed action, and they postulate an effect on the cytoplasm, producing a tension that acts on the chromosomes later. Such cytoplasmic mediation may well be a part also of the process of mutation of the genes.

X-Ray Lethals. While the mutations produced by X rays have been of many kinds, both structural and physiological, lethal ones have been most studied. The reason is chiefly that absence of certain kinds of individuals is easier to detect than is a visible change in some unspecified part of the body. Muller made the first notable study of

X-ray-produced lethal mutations in Drosophila by means of what is
called the *ClB* X chromosome (Fig. 74). This chromosome contains
the repeat segment *B* for bar eye which, being semidominant, marks
any fly having this extra segment even once. The same chromosome
contains a lethal gene *l* which would kill a male because he has
only one X chromosome, but which does not affect a female if her other
X chromosome is normal. The symbol *C* stands for something which
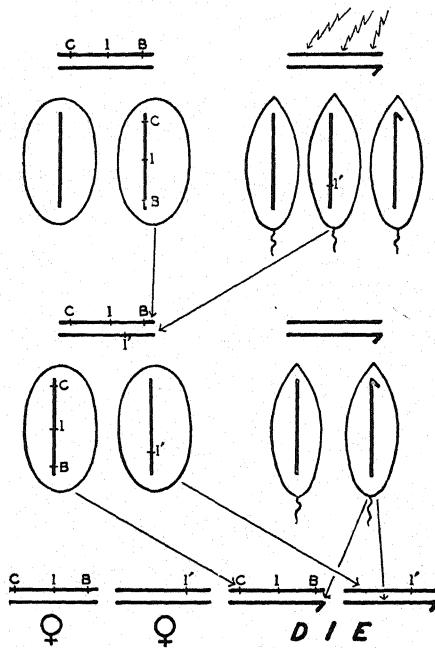
Fig. 74. Method of detecting lethal X-chromosome mutations in Drosophila after
irradiation of males, by means of *ClB* females.

prevents all crossing over between the two X chromosomes, so that
l and *B* remain always together. In a stock of such flies any female
with bar eye must also carry the lethal gene in the bar-marked chromo-
some. The male offspring of such a female would receive their one X
chromosome from their mother; those getting the *ClB* chromosome
would die, leaving only wild-type males and only half as many males
as expected.

Muller's experiments consisted in irradiating adult male flies in the
hope of producing lethal mutations in the X chromosome of some of
their spermatozoa. The irradiated males were then mated with

ClB females. If any of the male's X-bearing sperm did contain a lethal, which we may call *l'* since it would almost certainly be different from the *l* of the females, and if such a sperm fertilized a *ClB* egg, the constitution of the fertilized egg could be written *ClB/l'* (left center, Fig. 74). This symbolization means that one of the chromosomes of the pair contains *ClB*, the other contains *l'*. This fertilized egg would develop into a bar-eyed female. She would survive despite her two lethals, since the lethals are not homologous; each would be prevented from harming her by the normal gene opposite to it in the other X. There would be other bar-eyed females in the same family, but they would be *ClB/+*, in which the plus sign indicates a normal wild-type X chromosome from the irradiated father.

Numerous bar-eyed daughters of such irradiated males were mated, most of them *ClB/+*, some of them, Muller hoped, *ClB/l'*. It made no difference what kind of males they were mated with, since the only question at issue was the nature of their X chromosomes. Any *ClB/l'* female would produce no male offspring at all, since half the expected sons would be killed by the *l* in one of her X's, the other half killed by the *l'* induced by irradiation in the other X. It was easy to tell whether the offspring from any mating included any males. Every maleless progeny meant a lethal mutation in an X chromosome of the irradiated male's spermatozoa. A certain very small percentage of sonless progenies of *ClB* females occur naturally, without irradiation. Muller's experiments yielded, not just a statistically significant increase in such families, but 150 times as many as without irradiation. Most of the effect is on mature sperm; about five times as many lethals are produced in ripe as in unripe sperm at a dosage of 3000 r.

X-Ray Visible Mutations. While mutations produced in any irradiated male may be detected if the progeny are inbred through enough generations, visible mutations produced in the X chromosomes of Drosophila may be more quickly revealed by what are called attached-X females. The two X chromosomes of these females are attached at one end, so that they behave as a unit. Such females also contain a Y chromosome, and they may be symbolized by XX Y. Meiosis separates the Y from the two X's, so that eggs are of two kinds, XX and Y, respectively. Such eggs, if fertilized by X-bearing spermatozoa, yield XX X eggs (which usually perish) and XY eggs which become normal males. The X chromosomes of these males come, of course, from their fathers, not from their mothers as X chromosomes ordinarily do.

The experimental production of visible mutations starts with irradia-

tion of adult male flies (Fig. 75). These males are then mated with XX Y females. If a visible mutation, say the one for vermilion eye, is produced in one of the X-bearing sperm, and this sperm fertilizes a Y-bearing egg, the resulting male will have vermilion eyes. It takes a long time to examine the males all over, which must be done because any part of their organization may be changed. The amount of labor involved discourages this kind of experiment and is the reason why lethals have been looked for instead. But the XX Y tests have been made, and the excess of mutant males after irradiation over the mutant males occurring normally may be charged to the radiation.
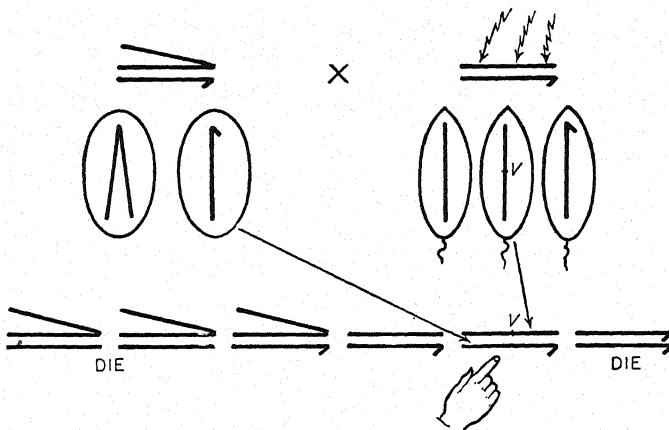
FIG. 75. Method of detecting visible X-chromosome mutations in Drosophila after irradiation of males, by means of attached-X females.

Less than one-tenth as many visibles have been discovered as lethals in a given number of tested X chromosomes.

Other Radiation. Ultraviolet has a moderate mutagenic effect at wave lengths shorter than about 3000 A., not much at lengths above 3130 A. (A. is the angstrom unit of wave length; it is one ten-thousandth of a micron, or one ten-millionth of a millimeter.) It does not ionize protein molecules; that is, it does not eject electrons, though it may excite them to greater energy. The nucleic acids of the proteins appear to be the receptive part of the genetic mechanism, for it is they that absorb the ultraviolet. Ultraviolet applied before and after X rays opposes chromosome aberrations, apparently by helping broken ends to rejoin "as they were." As an experimental agent it has the disadvantage of being absorbed by any tissue surrounding the germ cells; hence it is best for fungus spores, pollen grains, and similar small

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objects. Many physiological mutations in the bread mold Neurospora have been artificially induced by ultraviolet.

Pretreatment with near infrared (under 18,000 A.) increases the chromosome aberrations induced by X rays, even if it is applied some hours before the X radiation. This is not done by merely favoring the
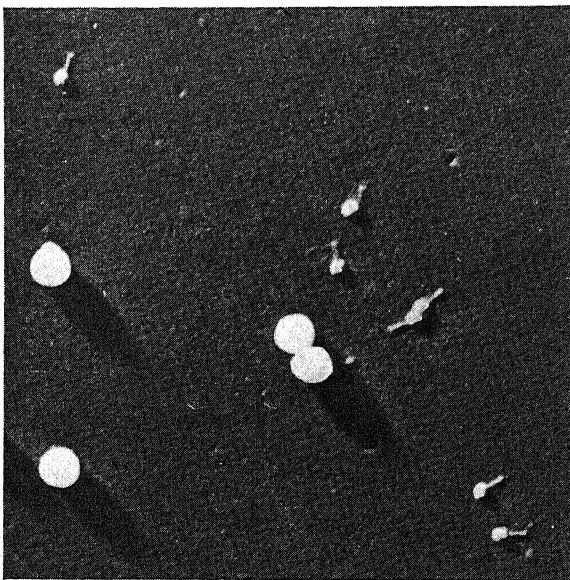
Fig. 76. Bacteriophage T2, resistance to which has arisen by mutation in the bacterium *Escherichia coli*. The seven knobs with handles, ranged from northwest to southeast, are the phages. The large white spheres are reference objects to determine magnification, which is 21,000 diameters. (*Electron micrograph by Professor Robley C. Williams.*)

union of *new* broken ends rather than the rejoining of those just separated; it actually increases the breakages.

Bacteria have also had their mutation rates greatly increased by ultraviolet. Resistance of bacteria to phages is one of the characters tested. Sensitive bacteria adsorb many of the phage particles (Fig. 76) on their surfaces, and some of these particles penetrate the bacterium where, after multiplying, they destroy it. Resistant bacteria do not adsorb the phage particles, and this type has arisen by mutation from the sensitive kind. Such mutations in one strain occur naturally in less than one in a hundred million divisions, but applying ultraviolet at a dosage of 1000 ergs per square millimeter increased the rate immedi-

ately more than twenty times. Mutations continued to happen after the treatment, but at a declining rate, until after about thirteen bacterial divisions it had returned to the spontaneous rate. Ultraviolet four times as strong as this raised the mutation rate to 70,000 times the normal. While the genetic mechanism of bacteria is not known, geneticists are assuming that genes and chromosomes exist in them until something is learned to refute that view.

Certain bacteria have gained, others have lost, by mutation the power to synthesize such substances as proline, cystine, and arginine, and ultraviolet has been the agent.

Temperature shocks, brief exposures of Drosophila larvae to approximately 38°C., have caused a number of mutations, some of them identical with mutations that had earlier arisen spontaneously. Cold shocks —freezing or below—have about as great an effect as heat-treatment. Low temperature at the time of X-raying favors *new* unions of broken ends, hence increases the resultant reorganization of chromosomes. High temperature increases the frequency of natural (spontaneous) mutation, but has no such effect on artificial X-ray changes. Neutron bombardment has been proved effective. Cosmic rays, once thought to produce a slight increase in mutation, now appear to have no such effect.

Atomic-bomb radiation was tested by exposing corn grains within the target area at Bikini on July 1, 1946. Plants grown from them were outcrossed to unexposed plants, and it was found that chromosomes were altered in about 5 per cent of the progenies. Barley and several kinds of wheat were subjected to comparable tests and the mutation rate raised to about fifteen times that of controls. By appropriate comparisons it was shown that the radiation effect there was somewhat over 15,000 r of X rays.

Other Agents Combined with Radiation. The efficiency of X rays may be increased by the use of certain other agents before the radiation. Introduction of salts of heavy metals into an organism, which is then exposed to X rays, has increased mutation above the amount produced by equivalent X rays alone. The effect of the heavy atoms is probably to increase the absorption of the energy of the rays. The spiderwort Tradescantia exposed to X rays in oxygen produced more chromosome aberrations than with the same dosage in air. Helium, argon, or nitrogen replacing air reduced the chromosome changes. Oxygen had about five times as much effect as nitrogen. A 5 per cent oxygen mixture at 2 atmospheres of pressure had about the same effect on X rays as did 10 per cent oxygen at 1 atmosphere; this indicates that

the increase of aberrations was really an oxygen effect. Production of sex-linked X-ray lethals in Drosophila is likewise increased in an oxygen atmosphere. Exposure of Tradescantia to 250 r of X rays and simultaneously subjecting it to sonic energy of 9100 cycles per second yielded about 1.3 times as many chromosome reorganizations as did the X rays alone. Conger, who reports this result, believes that the vibrations due to the sonic treatment merely kept more of the broken ends from rejoining the ends from which they had been torn, thus increasing the new unions. Pretreating the mold Neurospora with nitrogen mustard before applying ultraviolet increased both morphological and biochemical changes. These were gene mutations rather than chromosome breakages. Bathing plant tissues in a colchicine solution reduces X-ray-produced aberrations, probably because, by slowing down chromosome movements, it favors the reunion of parts of the same chromosome. Nucleic acid hinders breakage by X rays, but it has not been much used artificially; nucleic acid naturally accumulates on the chromosomes in certain phases of mitotic cell division, and breakages are at a minimum at those stages.

Drosophila fed on lead acetate, then X-rayed, produced a greater number of lethal mutations than without the acetate. The flies were also influenced by breeding them a number of generations on food mixed with a weak solution of tincture of jaborandi. After such treatment, X-raying at 2900 r produced twice as many lethals as without the pretreatment.

Radiation the Cause of Spontaneous Mutation? When the mutagenic effect of radiation in the laboratory was discovered, it promptly suggested that perhaps natural mutation is caused in this way. The earth is constantly giving off radiations because of radioactive substances in it. The possibility of testing this source arose from the proportionality, mentioned earlier, of dosage to amount of mutation—the greater the radiation dosage the more mutation, in a straight-line relation within a considerable range. The earth's radiation was measured and compared with the dosages which produced artificial mutations. From this comparison came the conclusion that only a small fraction of 1 per cent of the observed natural mutation could be accounted for by the earth's radioactivity. Organisms may concentrate radioactive substances in their tissues, but the amount can be measured, and after making allowance for such concentration there still is not nearly enough natural radioactivity to account for observed mutation. The cause of spontaneous changes must be something else. What that other thing may be is suggested later. There has been speculation over thermic excitation

of atoms which might on occasion overcome cohesion, but no facts are known that could raise the discussion much above conjecture.

Chemical Agents of Mutation. It would seem almost a foregone conclusion that mutation of genes, conceived to be a chemical change, could be influenced by chemical agents. Yet even in the year 1940 the evidence of any such action artificially initiated remained exceedingly confused. Many attempts had been made, some successes were claimed, some of the results (such as counts of lethals produced) were barely of statistical significance, and some repeated by other investigators were not verified. In some such experiments fungi reared on abnormal media gave the appearance of having mutated, but the results could be explained by assuming that mutations already present found the new media more favorable and they outgrew the wild type.

Undoubted mutations were, however, produced in numbers by various chemical substances by the middle 1940's, in experiments by English and American geneticists. One of the principal agents has been the mustards. There are two types of mustards, nitrogen and sulfur, differing in their central element. Both kinds are mutagenic. They have produced both lethal and visible mutations in Drosophila, about as abundantly as X rays. The treatment was given to the adult flies. The mold Neurospora has mutated visibly, and to loss of the capacity to synthesize certain substances, about as readily in response to nitrogen mustard as to X rays. The treatment was applied to the germinating conidia and other points of the mold cycle. Similar treatment of the fungus Coprinus destroyed, in four different mutations, its ability to synthesize four of the amino acids. The mustards have also reversed a biochemical mutation of Neurospora, thereby restoring to this mold its previously lost capacity to synthesize inositol. Bacteria subjected to nitrogen mustard lost their power to synthesize a number of the amino acids. Nitrogen mustard reduces viability of certain clones of Paramecium, and it is known that part of this effect is exerted through nuclear material (genes or chromosomes). Probably also it works through the cytoplasm, Paramecium being one of the organisms that has some sort of genetic mechanism outside the nucleus. And finally, injecting nitrogen mustard into the peritoneal cavity of mice was followed by production, in one among nine survivors of the treatment, of a mutation affecting ears, tail, and hair. This result will need to be based on more tests, but earlier injections of methylcholanthrene into mice had increased certain mutations more than fortyfold.

Other substances have proved likewise to be mutagenic. A few must suffice for illustration. Certain hydrocarbons have produced lethal mu-

tations in Drosophila, the most effective of them being dibenzanthra-
cene. Several azo compounds have had the same effect. Mutations of
the bacterium *Escherichia coli* have been induced by sodium desoxy-
cholate, neutral acriflavine, colchicine, caffeine, several carbamates,
and other substances. One investigator reported that after rearing a
bacterial species on a medium containing methionine the bacteria lost
the power to synthesize methionine. This effect may have been, not
mutation, but a result of selection; a strain of methionine-requiring
bacteria may have been in the culture, and in the presence of methi-
onine it outmultiplied the others. Camphor has increased two- or
threefold the mutation of yeast to certain types of giant colonies. Anti-
bodies, produced against Neurospora in serum of rabbits, have caused
a dozen mutations in Neurospora. The genes presumably guided the
production of the antibodies, in relation to their own configuration, and
were in turn modified by those closely fitting antibodies. Ovaries re-
moved from Drosophila larvae, bathed in a solution of phenol, and then
transplanted to other larvae, produced in the "offspring" of the host
fly about 20 per cent of mutations in the second chromosome, as against
a fraction of 1 per cent in the controls. Most but not all of the muta-
tions were lethals. Certain loci of the second chromosome mutated re-
peatedly, indicating either a specificity of the action of phenol or, more
likely, a greater sensitivity of these loci to mutagenic agents in general.
Urethane has been injected into the bodies of adult male Drosophila,
and the offspring of such males were tested for mutations by the *ClB*
method. The mutations were 6 to 16 times as frequent as in the controls,
and among them the lethals were 4 or 5 times as abundant as the visible
ones. Some of the changes were small deletions, as shown by the
salivary-gland chromosomes, but most of them involved no visible
change in these chromosomes and were regarded as gene mutations.

Lastly, peroxides were found to be mutagenic, first as a by-product
of ultraviolet treatment. Irradiation of the medium on which bacteria
were raised produced peroxides in that medium, and later direct ap-
plication of hydrogen peroxide to the mold Neurospora induced muta-
tions in it. The effect of the peroxide was milder, however, than that of
ultraviolet treatment; hence the radiation must work in other ways
besides producing peroxides.

An interesting by-product of the evolutionary study of artificial mu-
tation is the attempt to relate such mutation to cancer of the higher
animals. A current theory holds that cancer is the result of the produc-
tion, in various kinds of body cells, of mutations which destroy the
ordinary restraints of growth. Latarjet and others have tested two

groups of related substances (a series of carbamic acid esters, and a group of water-soluble derivatives of hydrocarbons) in each of which some substances are cancer-producing, others not. They found that in both groups the substances which induce cancer also cause mutation in the resistance of the bacterium *Escherichia coli* to the virus T1, while the noncarcinogenic substances of both groups do not cause the bacterial mutations.

Genetic Control of Mutation. Some of the agents causing or hastening mutation are within the organism itself. Other genes are among these. A clear case is the "dotted" gene (*Dt*) in corn. Its one known effect is to cause frequent mutation of the gene *a* lying in a different chromosome. The gene *a* is transformed into *A* which produces anthocyanin pigmentation. Another example is the "miniature" gene of *Drosophila virilis.* In some strains this gene is fairly stable; in other strains it often mutates back to the wild type. This difference in strains is partly due to differences in the miniature gene itself in the various strains; but it also depends on four other genes located in different chromosomes, and these genes are not equally represented in the different Drosophila strains. In another species of Drosophila a strain from Florida mutates more frequently than others. The cause of this is a gene in the second chromosome. Stocks homozygous for this gene mutate ten times as often, those heterozygous for it two to seven times as frequently, as do stocks not having the gene at all. The same gene also causes inversions in chromosomes. Its effect is general, favoring mutation of many different genes, though it influences some genes more than others.

In *D. pseudoobscura* there is a mutation-inducing gene in the second chromosome, but it does not work unless a Y chromosome is present— that is, ordinarily in a male. The Y chromosome of one species has been shown to increase mutation in another species to which the Y was introduced by a cross.

The influence of genes upon mutation of other genes opens up tremendous possibilities of evolution. A species could almost evolve itself into another type of organism if somehow it got the right genes in the first place.

Polyploidy. Since repeats and other duplications of chromosome segments produce changes in the appearance of organisms, it would be expected that duplication of *all* the genes would have an even more marked influence. In fact, such duplication of all genes was known long before the doubling of a few genes was discovered, and it was observed that appearance did change. The condition produced by this

duplication is known as *polyploidy*. In general, polyploidy is brought about by duplication of the chromosomes for cell division, after which the cell fails to divide. If this duplication occurs in a diploid cell, the resulting cell is said to be tetraploid. Other multiples of a basic number may be produced, and suitable prefixes indicate the extent of the duplication.

One way of producing polyploidy is through regeneration at a wound. If a tomato plant is cut off, buds starting at the cut surface
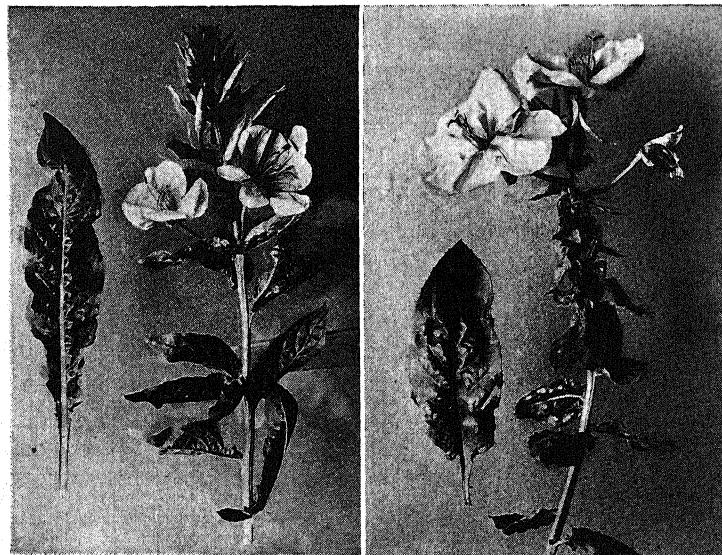
Fig. 77. Flowers and leaves of *Oenothera lamarckiana* and the tetraploid *O. gigas* (*right*). (*Photograph by Professor B. M. Davis.*)

sometimes have the doubled number of chromosomes. This number is 48, instead of the diploid 24 characteristic of the tomato. Shoots produced from such buds may be grown as cuttings, produce flowers where eggs and pollen have 24 chromosomes in place of the usual 12, and a permanent tetraploid type results.

Many polyploid forms have been produced in plants by immersing parts of them in solutions of colchicine. This substance is extracted from the autumn crocus Colchicum. Other agents effecting such doubling are acenaphthene and indole acetic acid. Curiously enough, Colchicum cannot be made tetraploid by colchicine, but its chromosomes can be so doubled by acenaphthene. Colchicine applied to Drosophila larvae induced tetraploidy in some spermatogonia and oögonia, but no

tetraploid flies were obtained in this way. Low temperature (freezing or below) made a fraction of 1 per cent of Drosophila females triploid, a conclusion that was confirmed by appropriate crosses.

In general, tetraploid plants have thicker leaves, larger flowers (Fig. 77), and larger fruits. The plant as a whole may be smaller (Fig. 78) or larger, and less or more vigorous, than diploids. The larger flowers have appealed to plant breeders, and many new colchicine-produced cultivated tetraploids are already in existence. It is advantageous, some-

FIG. 78. Size and habit of growth of *Oenothera lamarckiana* (*left*) and the tetraploid *O. gigas*. (*Photograph by Professor B. M. Davis.*)

times necessary, to propagate such forms vegetatively because tetraploids are usually less fertile than their parent diploids and the new tetraploid number of chromosomes is not maintained.

Triploid plants may be produced when the doubling of the chromosomes occurs in the egg, which is itself thus diploid. If this egg is fertilized by normal haploid pollen, the chromosome number is one-half greater than the diploid. Triploids are also produced by crossing tetraploid with diploid species. This has been done with the two Oenothera species contrasted in Figs. 77 and 78. *Oenothera gigas* is tetraploid; the common way of expressing tetraploidy and at the same time giving the number of chromosomes would be for this species 4n = 28. *O. lamarckiana*, on the contrary, is diploid, 2n = 14. These types of

plant have been crossed, and their hybrid has $14 + 7 = 21$ chromosomes ($3n = 21$). Exactly the same kind of Oenothera has been found in nature, where the mode of origin was unknown.

In the newt Triturus, Fankhouser has induced triploidy by heat applied to the eggs, in which entrance of the sperm normally occurs between the two divisions of meiosis. In heat-treatment the second meiotic spindle is well within the egg, not at the surface. The nucleus which would go into the second polar body is thus retained in the egg. The two nuclei formed by the second division are then joined by the sperm nucleus, which provides a total of 33 chromosomes (triploid). From the triploids an occasional tetraploid is obtained.

An advantage of polyploidy, in addition to the greater vigor which it often confers, is that it makes chromosome deletions or deficiencies less serious. Absence of a segment from one chromosome may cause little damage if there are three complete homologous chromosomes in each cell, while a sizable deficiency usually does harm if there is only one chromosome furnishing the normal complement of genes.

Difficulties of Polyploidy. Though tetraploidy often confers added vigor to a plant, it usually causes trouble in the production of germ cells. There are four chromosomes of each kind, and it is needful that they join in pairs. Chromosomes that pair can usually be counted on to go to different cells at meiosis, and if all chromosomes pair, all eggs and every pollen grain should have the same haploid chromosome content. Now, the *genes* of a tetraploid plant *do* in general pair. When two homologous genes pair, the attractive force which brings them together is nullified, and they do not attract the other two genes of the same kind. These other two genes then form another pair. So far as the genes are concerned, then, the union is two and two. All would be well if all the genes in one chromosome paired with their homologues in a single one of the other three chromosomes. The chromosomes would thus also pair two and two. But in most tetraploids, when first produced, that does not happen. In one segment of chromosome A the genes may pair with those of chromosome A'; then in a following segment the genes of A may pair with those of A". Farther along the chromosome the genes of A may pair with those of A'". At any one level the genes are paired two and two, but all four of the chromosomes may be brought into a loose group.

At meiosis, under these circumstances, the chromosomes will not be distributed equally to the cells. Some tetrads of chromosomes will separate by twos, but others will send three to one cell, one to the other. Chromosomes sometimes get lost and do not go to either cell. Eggs and

pollen will come to contain different numbers of chromosomes, and the offspring they would produce are often not viable. Fertility is thus reduced, sometimes drastically so. Triploids are in an even worse situation, because there is no way, even by accident, whereby the two cells produced at one meiotic division can be alike with respect to a given kind of chromosome—unless one chromosome is lost.

If a tetraploid type succeeds in maintaining itself for a number of generations, through the production in each generation of some normal eggs and pollen, one thing can happen to improve its prospects. Mutations may occur. These would happen in only one of the four genes at a time. Such mutations could alter the attraction of the genes for one another at meiosis, increasing that force for some, diminishing it for others. If such mutations gradually accumulated in the chromosomes in the right way, the time might come when a particular two of the four chromosomes would regularly constitute a pair at meiosis, the other two another pair. A plant containing such chromosomes would then be a functional diploid, even though it still contained 4n chromosomes as related to the number in an ancestor.

Allopolyploidy. In the preceding account it has been assumed that the polyploid condition arose through the multiplication of chromosomes within a single plant or in a more or less homogeneous group. The four chromosomes of one kind in a tetraploid produced in this way would all be pretty much alike. Not much evolution has come from such polyploidy; the advantages of the tetraploidy have been overshadowed by its difficulties. Quite different is the situation in which two groups of somewhat unlike chromosomes are brought together before their duplication. This happens in crosses between species, or between variant types within the same species.

If a species in which $2n = 26$ were crossed with one in which $2n = 18$, their hybrid would normally possess $13 + 9 = 22$ chromosomes. There might well be considerable homology between the genes of the two species, so that there could be some pairing of maternal and paternal chromosomes in the hybrid. But with even the best possible homology only 9 pairs of chromosomes would be formed, leaving 4 chromosomes unpaired. These would behave irregularly at meiosis, eggs and pollen would be of many kinds, and fertility would be low.

This situation could be corrected by doubling the chromosomes in the fertilized eggs, which would then contain 44 chromosomes. Every one of these chromosomes in the hybrid would then have a strict homologue—its sister chromosome produced at the duplication—and all chromosomes of the hybrid would pair. All would separate in the

same way in all meioses, and all eggs and pollen would be alike. Such a plant should be highly fertile so far as its fertility is determined by regularity of chromosome behavior. A polyploid formed in this way—the doubling of two unlike chromosome groups—is known as an *allopolyploid.*

A classical case of allopolyploidy, artificially produced, is that of the hybrid between radish and cabbage. These plants have the same number of chromosomes ($2n = 18$), but they belong to different genera, and any homology between their genes is of little influence in relation to attraction between them in meiosis. There are 18 chromosomes in the hybrid (Fig. 79), 9 from the radish and 9 from cabbage, but they do not pair. As a result its germ cells receive various numbers of
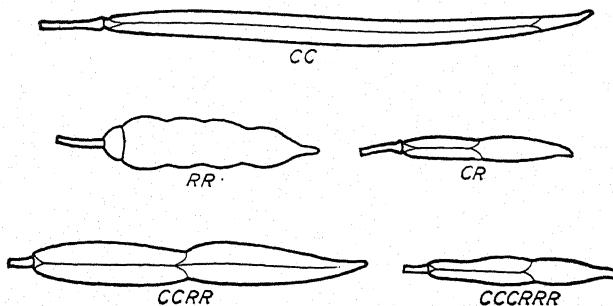
FIG. 79. Seed capsules of cabbage (*CC*), radish (*RR*), their diploid hybrid (*CR*), and two of their allopolyploids. The two capsules, *below,* are, respectively, tetraploid and approximately hexaploid.

chromosomes, mostly from 6 to 12, and the hybrid is nearly sterile. However, a few of the reproductive cells whose division is typically meiotic fail to divide after their chromosomes are duplicated. Each final germ cell of such origin accordingly has 18 chromosomes, 9 radish and 9 cabbage. A fertilized egg from this source would have 36 chromosomes, 18 radish and 18 cabbage. In it the chromosomes can pair, the 18 radish chromosomes entering into 9 pairs, the 18 from cabbage forming 9 other pairs. Such a plant is fully fertile. Approximate hexaploids with lower fertility have also been produced.

A wheat-rye hybrid has been several times produced artificially and preserved as an allopolyploid. In tobacco, *Nicotiana tabacum* is an allopolyploid from a cross between *N. sylvestris* and *N. tomentosiformis,* though certain differences between natural *N. tabacum* and the artificially produced allopolyploid indicate that mutations have occurred in the former.
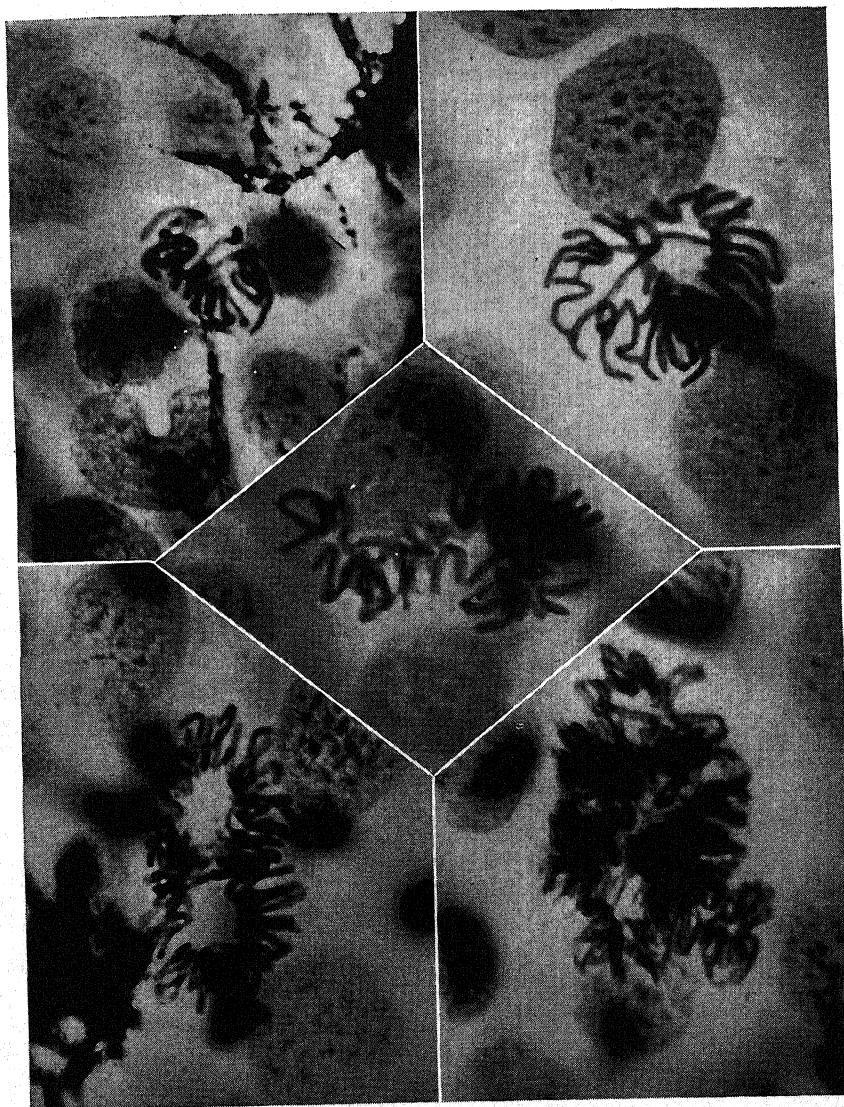
FIG. 80. Polyploid chromosome groups in tail of the newt, *Triturus torosus*. Haploid, diploid (the normal), triploid, tetraploid, and octoploid nuclei are shown. (*Courtesy of Professor Donald P. Costello.*)

Polyploidy Rare in Animals. It is not accidental that most of our examples of polyploid organisms have so far been plants. Animals seldom produce them. That is not because their cells never fail to divide after chromosomes have duplicated, for polyploid cells are often produced, notably in the amphibia (Fig. 80). It is simply that something in animals prevents the polyploids from becoming established as separate types.

Many years ago Muller pointed out an obstacle to the formation of polyploid animals. The difficulty, he conceived, lay in the sex-determining mechanism. In most animals one sex produces two kinds of germ cells, one male-determining, the other female-determining. In mammals and most insects it is the male which produces the two kinds, while in birds and moths it is the female. The principle involved will be illustrated by the mammalian type—two kinds of spermatozoa in the male.

In the female mammal there are two chromosomes of a particular kind known as the X. She is a female *because* she has two of them—in relation to something else, presumably the other kinds of chromosomes. The male has only one X, but often another kind of chromosome known as the Y. The X and Y are not completely homologous, but they manage to go very regularly to different cells at meiosis. In man, the X and Y look as in Fig. 81 at

Fig. 81. Chromosomes associated with sex in man, the X at *top*, Y near *bottom*. (*From Painter in Journal of Experimental Zoology.*)

meiosis. Half the spermatozoa receive the X chromosome, half the Y. All eggs contain X. An egg fertilized by an X-bearing sperm will contain two X's and become a female; an egg fertilized by a Y-bearing sperm would contain X and Y and become a male.

Now, suppose such an animal becomes tetraploid. A female would be XXXX; by good luck these chromosomes might pair two and two and all eggs be XX, but without such luck eggs would have X or XXX. That, however, is not the main trouble. A male becoming tetraploid would be XXYY. Because their homology is slight, X and Y would probably never pair at meiosis; the pairs would be XX and YY. The paired chromosomes would go to different cells, and all spermatozoa would be alike, XY, not of two kinds as in actual animals. The XX eggs would be fertilized by XY sperm, and all individuals should be alike, XXXY.

What kind of sex development that chromosome group would produce can only be conjectured, but it should be the same sex for all. There should not be two distinct sexes any more.

This expectation that in polyploid animals all individuals would be of the same sex may suggest that hermaphroditic or parthenogenetic species might be or become polyploid, or perhaps that polyploids might become hermaphroditic or parthenogenetic. In hermaphroditic species, each individual produces both eggs and spermatozoa, and all individuals are alike in that respect. In parthenogenesis the eggs develop without fertilization, and there are species, largely among insects, in which all individuals are alike—we call them females. Probably a more pertinent comment in relation to species having separate sexes is that polyploidy, if it arose, would do so in just one individual at a time. This individual, if it were to leave descendants, would have to mate with one not like itself. The mating of a tetraploid with a diploid would produce an unbalanced hybrid which would have little chance of perpetuating itself.

Whether there are polyploid animals, or in what groups they exist, is a question more appropriately deferred to the next chapter.

Other Chromosome Numbers. Complete polyploidy is not the only way in which chromosome numbers may be increased. Through failure of maternal and paternal chromosomes of one pair to separate at meiosis (*nondisjunction*), an egg may possess one more chromosome than the usual haploid group. In Drosophila, eggs or spermatozoa have been produced with an extra X chromosome, or with an additional small fourth chromosome. If such a germ cell unites with a normal haploid cell in fertilization, a fertilized egg having $2n + 1$ chromosomes results, and from it sometimes a $2n + 1$ fly whose appearance is different. An individual with one extra chromosome of one kind, making three of that kind, is called a *trisomic*.

In the Jimson weed Datura, trisomics are not rare. This plant has 24 chromosomes, which means 12 kinds, and the extra chromosome may be any one of the 12. Accordingly, there are 12 different kinds of trisomics. They have different seed capsules (Fig. 82) and other characteristics, so that by appearance alone an expert may tell which chromosome is added.

The trisomic condition may also arise out of general polyploidy, rather than by nondisjunction of a single pair. A triploid, for example, produces germ cells containing various numbers of chromosomes. Some of these numbers are just one more than the haploid. Indeed, trisomy arising out of polyploidy may offer a better chance of evolution

than does an origin out of nondisjunction. A trisomic is unbalanced, and is for that reason not likely to become established. Theoretically it might lead to a balanced, perhaps successful, type if, instead of just one extra chromosome, it could get two extras of the same kind. Whatever
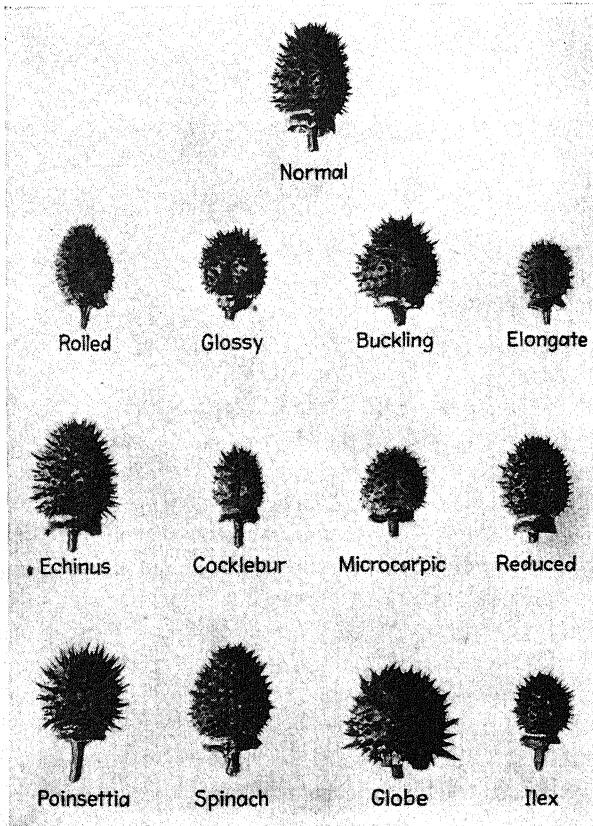
Fig. 82. Seed capsule of normal 2n Datura, *top,* those of its twelve 2n + 1 varieties, *below.* (*Courtesy of Professor A. F. Blakeslee.*)

difficulty a trisomic has merely because of an imbalance of chromosome number should be obviated by getting a second extra, so that the extras could pair at meiosis. Getting a pair of extras should be more readily done out of polyploidy than out of simple nondisjunction, because in self-fertilizing organisms, such as many plants, both egg and sperm of the same individual may have the extra chromosome. If such an egg

and sperm met in fertilization—not too likely but still possible—a type with two extra homologous chromosomes could arise.

Merely balancing chromosome numbers, so as to have even numbers, is not, however, guaranteed to produce a successful step in evolution. Four chromosomes of one kind have the same difficulty as do four chromosomes of *every* kind (complete tetraploidy). They may not pair two and two at meiosis. Moreover, pairing is not the whole trouble. Extra chromosomes may have other deleterious effects besides producing irregularities of meiosis. Drosophila can endure an extra small fourth chromosome, as indicated earlier; but two extra fourth chromosomes are fatal.

Additions of more than two to the 2n chromosome group may be accomplished, no doubt, by successive steps like the one just described. Another way would be by general polyploidy followed by the loss of some of the chromosomes. Loss of certain chromosomes when there are, say, four of a kind should not be a serious change. Mere change of numbers could be brought about by chromosome reorganization. There are indications that chromosomes have been joined, thereby reducing the number. An increase in number would require the division of a centromere, for chromosomes without centromeres are lost at division.

Evolution must, in one way or another, have involved numbers of chromosomes many times, for in animal species the number ranges from 2n = 2 in a nematode worm Ascaris to 2n = 224 in the geometrid moth Phigalia. Most of the even numbers, and many of the odd ones, below 100 are possessed by one or more species.

CHAPTER IX

GENETIC VARIATION IN WILD POPULATIONS

> . . . the organic diversity existing in nature, the differences
> between individuals, races, and species, are experimentally re-
> solvable into genic and chromosomal elements, which resemble
> in all respects the mutations and the chromosomal changes that
> arise in the laboratory.
>
> —Th. Dobzhansky, 1941

The types of genic and chromosomal change described in the pre-
ceding chapter provide, theoretically, the source of variation which
might lead to much evolution. Whether they do lead to change of
species is a question still to be discussed.

When geneticists first began to point to mutations as likely starts of
evolution, other biologists commonly rejected them on the ground that
they were laboratory products. The same attitude toward indoor phe-
nomena, as if they could not bear confinement within walls or fences,
had long before been shown in relation to animal breeding. Animals
under domestication were considered to vary in ways that had no
bearing on natural evolution. Mutations as the beginnings of evolution
were long rejected by as eminent a geneticist as Bateson, in England,
on the ground that mutant individuals could always be crossed with
the type from which they sprang. How, Bateson asked, could species
that are intersterile be separated by means of mutations that are always
interfertile? The answer to his question belongs in the chapter on Iso-
lation; its bearing here is merely his conclusion that evolution of species
did not begin with mutations.

After 27 years of exposure to rediscovered Mendelism an eminent
paleontologist still believed that mutations were something that hap-
pened in bottles, test tubes, and cages because of living conditions.
And after 50 years of revived Mendelism, one eminent geneticist still
holds that mutations of the kinds one observes do not differentiate spe-
cies. He looks to them as the source of variability *within* species but
as having nothing to do with separation of species. For the latter schism

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he postulates a much more radical change which he does not specifically describe and which no one has knowingly witnessed either in the laboratory or in nature. This view is not supported by many others; its validity should be judged by the student after examining the next several chapters.

If mutation *is* the starting point of evolution, natural populations should show variation. The variant characters should be transmitted as genes in the laboratory are transmitted; that is, they should show the sort of segregative inheritance which results from meiosis of chromosomes. Finding natural variation that is inherited in Mendelian manner does not exactly prove that it has arisen by mutation; yet one who adds two and two should not, without good reason, reject four as the answer. The only alternative would be to conclude that the variation has always existed, a view once promulgated by Lotsy.

Natural Variation in Drosophila. It is inevitable that genetically well-known organisms should furnish material for comparison between natural and indoor phenomena. Drosophila's share in this attention is no more than proportional to its share in the advancement of genetics. The early studies were merely examinations of numerous collected flies to see what differences they exhibited. In the most common laboratory species, *Drosophila melanogaster,* collections made in the late 1920's by a Russian worker revealed slightly over 2 per cent of individuals with some sort of visible deviation from the usual. The greatest number of these were changes in the number, size, or shape of bristles. Next most abundant were sizes and shapes of the eyes. Eye colors, modified wing veins, shapes of wings or legs were less common. Some of these features were environmental products and did not appear in later generations, but many of them proved to be mutations.

Later tests involved breeding the collected flies, so that results could be stated as proportions of chromosomes, not individuals, containing mutant genes. Ives found, for this same species, that in flies collected in New England, Ohio, and Florida, 55 per cent of the second—one of the two long—chromosomes contained lethal or at least deleterious genes. Most of them were at different loci in the chromosomes; that is, a fly could have a lethal in each second chromosome and not be homozygous for it. Figure 83 shows that even six lethal mutations in one pair of chromosomes need not produce a lethal effect *if* the mutations are strictly recessive. From the lack of homology among the lethals Ives concluded that they had arisen independently—that they had not been multiplied from a much smaller number of original mutations. Spencer found 20 visible (not lethal) mutations in 408 chromosomes of the sec-

ond and third pairs together, and there was little duplication among them.

Sex-linked characters—those whose genes are in the X chromosome— were studied by Berg. Among 1282 males collected in nature, 7 showed visible mutations in the X. Counting the males is counting the genes, for a male, having only one X chromosome, reveals any genes in it whether they are recessive or dominant. Females collected at the same place were bred in the laboratory and produced about the same proportion of mutant males as were collected in the wild population. In Italy, one investigator found the sex-linked vermilion and yellow genes in nature in numbers which suggested that they were useful to the flies which carried them. The mutation rate had been ascertained, and
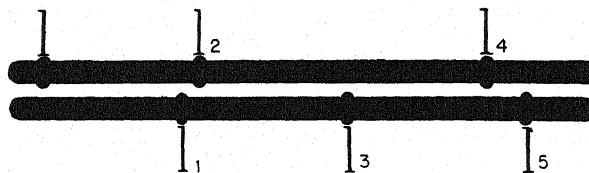
FIG. 83. Pair of chromosomes containing six lethals but not homozygous for any of them.

the flies with these genes were more abundant than mere neutrality should have made them.

The published numbers of natural mutations in *D. pseudoobscura* probably include some from *D. persimilis,* which was formerly not distinguished from *pseudoobscura.* A number of investigators have reported mutations of these species in nature at rates ranging from 10 to 20 per cent, or even to 30 per cent, of the chromosomes, some in the second chromosome, many more in the third. One of them estimates that less than 3 per cent of the flies have *no* harmful mutation in either of these chromosome pairs. The frequency of these mutations is a function, not so much of the rate at which mutations are produced, as of the amount of migration, the size of the breeding population, the extent of inbreeding, and the favor or disfavor shown by selection.

Other species for which censuses have been taken are *D. subobscura* (36 autosomal, that is, not sex-linked, mutations in 97 females), *D. immigrans* (16 visible mutations from 60 wild flies), *D. robusta* (89 visibles from 632 flies), and *D. hydei* (120 vermilion-eyed males among 1843). The last item may not represent wild conditions, since the flies were collected near a college town in which a genetics laboratory may have allowed vermilion flies to escape.

Before leaving Drosophila, for the satisfaction of those who believe that biological phenomena happening near man are somehow unnatural, we should point out that with the exception of *robusta* the Drosophila species named above have been introduced and supported by human activities—carried by man's commerce, maintained by his garbage. Geneticists do not think that the flies' contribution to an understanding of evolution is vitiated by their nearness to human beings.

Natural Variation in Other Organisms. Among mammals, Dunn has pointed out the similarity of variations found in nature to the mutations in the laboratory. Rodents of several kinds—mice, rabbits, guinea pigs —produce in nature individuals showing albinism, yellow or black coats,
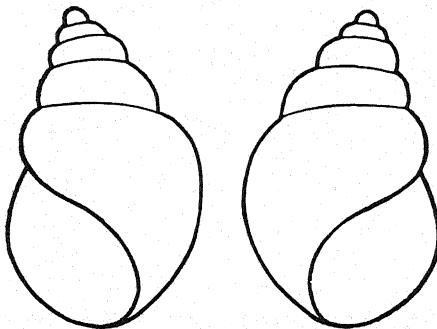
Fig. 84. Dextral (*right*) and sinistral snail shells, a one-gene difference.

pink eyes, or white spots. Some of these have been shown to be identical with laboratory mutations, though the expense of rearing precludes the kind of study done on Drosophila.

The western pocket gopher *Thomomys bottae*, according to Storer and Gregory, includes seven different types which resemble mutants of other rodents in the laboratory. The gophers, of course, have not been reared for genetic work. The hamster exists in a black and a spotted form. The mouse Peromyscus when brought into the laboratory and bred several generations often reveals some variant types. The subsequent mutation rate in these mice is so low that these early variants can hardly be attributed to mutations occurring after they were brought indoors; the new types must chiefly come from recessive genes already present.

Snails of some species have either dextral or sinistral shells (Fig. 84). While these distinctions have not arisen as mutations under observation, the physical basis of the direction of coiling has been localized in

the cytoplasm of the egg and is controlled by a single pair of genes with delayed action. It is assumed that one gene may mutate into the other. Lady beetles exhibit many differences in their patterns of spots and bands which are inherited as simple one-gene contrasts.

Meadow grasses, white mustard, and corn, in inbred generations, often show defects of their chlorophyll, dwarf plants, and other varia- tions which are approximately recessive, often simple, characters. These are cultivated plants whose wild ancestors are beyond reach and whose breeding follows from their economic value.

Variation Related to Taxonomy. Natural mutations coming to the attention of taxonomists—biologists whose interest lies in classifying organisms—are regarded in different lights, depending on their fre- quency, their location, and their miscibility with one another in popula- tions. Some of them are merely individual variability, as are blue eyes in man, or brown color in the black bear. Sometimes such forms are called phases. If two or more phases are rather common, the species may be said to be polymorphic. A common aphid growing on rose- bushes and potato plants consists of a pink and a green kind, each starting in the spring from a fertilized egg and maintaining its color through all the parthenogenetic generations which follow. Mutation must have produced this distinction.

When there is some spatial separation of two or more phases of a species, the groups are commonly called races. If the spatial separation is not sharply defined, that name is not usually applied, but the prin- ciple on which race rests is recognized. In man the A and B antigens in the red blood cells are each determined by one gene, one or both of which presumably arose by mutation. Red cells may contain one or the other antigen, or both, or neither. People having B are much more abundant in southeastern Asia, A is more abundant in western Europe, while North American Indians mostly have neither. One group of con- trasted genes does not suffice to establish races, but it helps.

The lady beetle *Harmonia axyridis* has a number of variations in its pattern of spots, which mark its races in different parts of Asia. The bird *Pachycephala pectoralis* has genes which produce yellow or black forehead, black or olive back, white or yellow throat, and black or colored wing, and there may or may not be a band on the breast. These contrasted characters, which must come from mutations, are combined in eight different ways on various South Sea islands. The gypsy moth is shown to have different genes related to sex, and these are distributed variously over the range of the species. If moths from different areas are crossed, they sometimes produce abnormal types known as inter-

sexes. The variation of the sex genes must be a result of natural mutation.

When closely similar species can be crossed, it is often possible to show that some of the differences between them rest on identifiable genes. Two species of lady beetle, *Hippodamia convergens* and *H. quinquesignata*, have been thus crossed. The differences between their patterns consist mostly of two bands in the latter species, each replacing two spots in the former (Fig. 85). One of these bands passes across the anterior end of each wing cover, the other just behind the middle. The anterior band is distinguished from two spots by just one gene, the band being dominant. The postmedian band may be as simple as that, but this is not quite certain. These species distinctions presumably rest on mutations of genes.

FIG. 85. Pattern of left wing cover of two species of lady beetles, *Hippodamia quinquesignata* and *H. convergens.*

The black form of the pocket gopher, one of seven types referred to earlier, is rare in California, but is paralleled in another species of the same genus in Idaho in which the black form is common, and in still another species in Oregon which is regularly black. These species have not been crossed, but it seems likely that the same mutant gene provides the black color in all three. Numerous other examples of parallel variation, as such correspondences are called, are on record, and in all of them similar or identical mutations are held to be the cause.

In Drosophila it is sometimes possible to cross two species and prove that a mutation occurring in them separately depends on the same gene in each. If the hybrid has the same *phenotype* (appearance) as the two mutant parents had, the mutations of the parents were identical. The ruby-eye mutation and a number of others in *Drosophila simulans* have been thus shown to be identical with mutations in *D. melanogaster*. This correspondence is not related to taxonomy, however, for the mutations do not constitute specific distinctions.

Many plant species can be crossed, and some of the crosses provide evidence that species are distinguished by gene mutations. So much species hybridization in plants, however, results in polyploidy that its consequences are left to a later section.

Chromosomal Inversions in Nature. Of the various kinds of major chromosome aberrations, inversions have been the most useful in the study of wild populations. Proving their existence is most easily done by visual identification; hence most of the natural inversions have been discovered in flies, whose salivary-gland chromosomes furnish the evidence. In plants, corn and spiderworts are favorite material.

The most fruitful study is that of *D. pseudoobscura* and *D. persimilis* by Dobzhansky. These flies are very closely similar, having once been
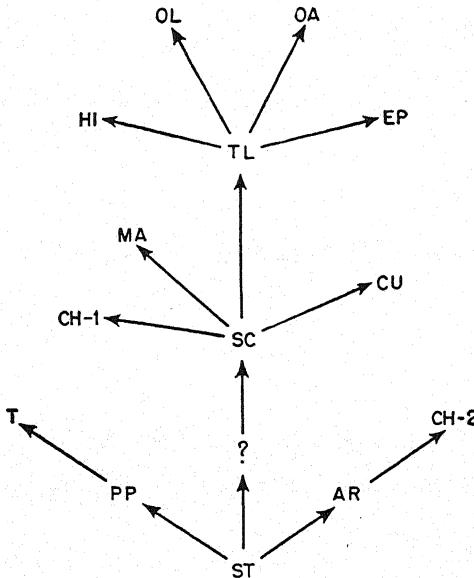
FIG. 86. Pedigree of third-chromosome patterns in *Drosophila pseudoobscura* as determined from inversions. AR, Arrowhead race; CH-1 and CH-2, two Chiricahua races; CU, Cuernavaca; EP, Estes Park; HI, Hidalgo; M, Mammoth; OA, Oaxaca; OL, Olympic; PP, Pikes Peak; SC, Santa Cruz; ST, Standard; T, Texas; TL, Tree Line.

regarded as the same species. The third chromosome of these species has experienced many inversions, and many different arrangements of the bands in the salivary-gland chromosomes are discovered in wild populations. The varying arrangements have a relation to one another such that one pattern may have sprung from another by means of a single inversion. The principle involved may be understood by referring back to the simple series of inversions in Fig. 68. The third chromosome of that figure (ABCGEFDHJ) could be derived from the second one (ABCGFEDHJ) by one inversion, as shown in the illustration. It

could not, however, be derived from the first one (ABCDEFGHJ) by a single inversion; a minimum of two inversions would be necessary.

Dobzhansky compared the patterns of the third chromosome found in many different areas in western United States, and was able to arrange many of them in a branching series built upon inversion as the method of change. That series, for *D. pseudoobscura*, is shown in Fig. 86. The patterns are mostly named from the areas where they were found, and the place names are abbreviated in the chart. At the base of the diagram is the pattern known as "standard" (ST) which may well be the ancestral type from which the others have stepwise sprung. From the standard, the Pikes Peak pattern (PP) could be derived by one inversion; likewise the Arrowhead pattern (AR) could come from standard by one inversion, but a different inversion from that producing Pikes Peak. These two derived patterns could each, by just one inversion, give rise to another discovered pattern (T and CH–2, respectively). Farther up the diagram Santa Cruz (SC) differs from four others by one inversion each, and one of these four, Tree Line (TL),

FIG. 87. Third-chromosome pedigree of *Drosophila persimilis*, based on inversions. CO, Cowichan race; HU, Humboldt; ME, Mendocino; SE-1, SE-2, two Sequoia races; ST, Standard; W, Wawona.

differs from four additional patterns by just one inversion different for each of the four.

Standard and Santa Cruz could not be changed, the one into the other, by a single inversion, but would require two. It is postulated that a pattern represented by the question mark resulted from one inversion and that it then experienced the second inversion. The postulated pattern has not been found, but it may exist where no collection has yet been made. Almost exactly the hypothetical pattern does exist in another species, *D. miranda;* the latter species may well be connected, in its origin, with *pseudoobscura*. Of interest in connection with this missing pattern is the fact that, as the chart of relations grew, Santa Cruz and Tree Line were question marks at first. They were found in nature after their existence had been postulated as necessary.

The inversion chart *could* be interpreted as beginning at any one of the patterns. Any pattern connected with it by an arrow—the direction the arrow points is arbitrary—could be derived from it by one

inversion. The "tree" could be turned upside down. One reason for putting the standard pattern at the base is that that pattern is also found in *D. persimilis*. In this latter species other inversions are involved (Fig. 87). Standard could be converted into three others, each by one inversion; and one of these could be changed into four more patterns by just one inversion for each one.

Inversions in these two species not only furnish a likely mechanism of evolution; they even make possible the tracing of probable lines of descent. For some reason the other chromosomes (besides the third) in these species are less changeable; yet enough rearrangements of the
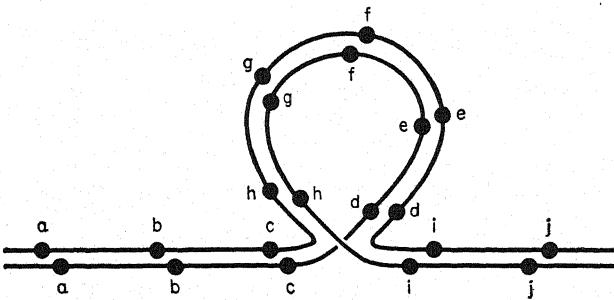
FIG. 88. The loop produced in the pairing of two chromosomes heterozygous for an inverted segment.

second chromosome are known to provide a small tree of descent for it also.

Inversions have been observed in the midges (Chironomus), which likewise have patterned salivary-gland chromosomes. In other organisms, in the absence of visible pattern, inversions are detected by chromosome loops. In an individual whose two chromosomes of one pair differ by an inversion, these two chromosomes pair in meiosis by means of a loop (Fig. 88). The chromosomes pass around this loop in opposite directions, so that homologous genes will be side by side. Such loops are sometimes seen in corn, in individual plants which must be inversion heterozygotes. Other plants showing chromosome loops are stocks, rye, trillium, certain lilies, spiderworts, and peonies. Even man gives some indication of inversions, but the evidence involves cytological phenomena too complicated to present here.

From the frequency with which high mutation rates in Drosophila stocks are associated with inversions, Ives concludes that the inversions may be the cause of much spontaneous mutation. Since large outbreeding natural populations should carry a larger percentage of inversions

than small inbred laboratory populations could retain, he suggested that the bulk of natural mutation may be thus genetically induced.

Translocations in Wild Populations. Though translocations have not been so spectacularly useful in tracing lines of evolution, they have been demonstrated to have evolutionary significance. One plant which has revealed such changes is the Jimson weed Datura, whose trisomic types have already engaged our attention. Blakeslee has portrayed the translocations as carrying half chromosomes to new places. While the breakages may not have been so regular as that, half chromosomes are convenient units for illustration. The 12 kinds of chromosomes of this species would thus consist of 24 half chromosomes which may be numbered from 1 to 24. One chromosome would be made up of the first two of these and could be designated 1·2, another chromosome 3·4, and and so on. Let us examine a translocation involving exchanges among three chromosomes, 1·2, 3·4, and 5·6. A "normal" plant, in its diploid cells, would have these chromosomes in the numbered combinations shown at the upper left in Fig. 89. Suppose, now, that the six half chromosomes have joined in a new way and that a race of plants homozygous for the new arrangement, as at the upper right of the figure, has become established. If the normal type is crossed with this new translocation type, their hybrid will have the six chromosomes shown in the center. These chromosomes are not shown as pairs, since no chromosome is homologous with any other chromosome throughout its length.

When meiosis occurs in this hybrid, its chromosomes will have to pair as in the star-shaped pattern at the lower left of Fig. 89, in order to bring homologous genes together. Then as the chromosomes begin to separate, they open up into a ring as shown at the right, with adjacent chromosomes in the ring going to opposite ends of the spindle.

How such translocations complicate the genetic phenomena is beyond the scope of this book. Our interest is in the demonstration that translocations have occurred in nature. The translocations that occur in salivary-gland chromosomes of flies can be seen and recognized as such. In species without such visible patterns the occurrence of chromosome figures like those at the bottom of Fig. 89 is evidence of heterozygous translocations. Corn, peas, stocks, peonies, and a number of other plants have shown these chromosome rings. The evening primrose Oenothera, whose genetic phenomena are of a very different sort from most of the rest of the plant world, owes this peculiarity to numerous translocations. In some species of this plant, all the chromosomes join in one large ring at meiosis; in other species many of the

chromosomes form a ring; the rest remain as pairs. Some of the spe-
cies of Oenothera are perpetual heterozygotes—part of their peculiar
genetics—and show the chromosome rings regularly. In other organ-
isms the heterozygotes are occasional, and it is only in these that the
rings of chromosomes are observed.

Animals have furnished fewer known examples of translocations than
have plants. Grasshoppers and copepods are among those which occa-
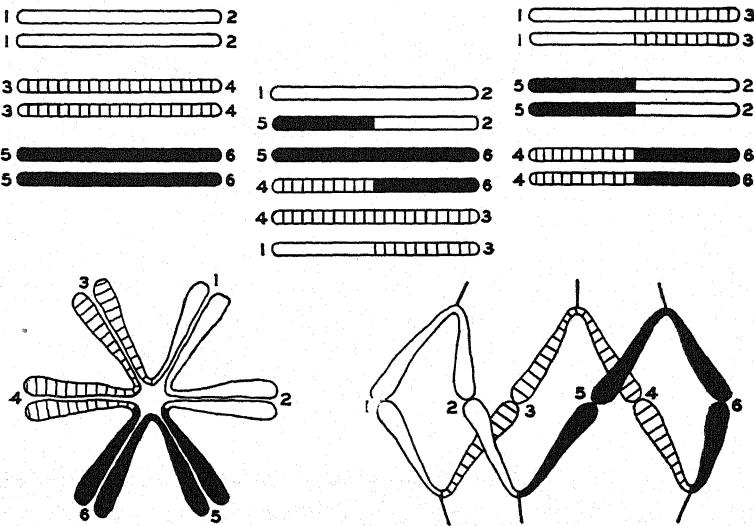
Fig. 89. Translocations among three chromosomes, and the pairing of these
chromosomes in a translocation heterozygote.

sionally reorganize their chromosomes in this way in natural popula-
tions. Shapes and sizes of chromosomes may be greatly altered by the
various chromosome aberrations, and translocations presumably share
the responsibility for such changes. They help to explain the different
appearance of the chromosomes even in very closely related species.

Other Natural Aberrations. Repeats or other duplications, or defi-
ciencies, or both, are almost certainly the basis of different forms of the
Y chromosome in *Drosophila pseudoobscura*. Seven distinct types of Y
are known in this species, occupying different areas. They differ in
length, the longest being nearly twice as long as the shortest. They also
differ in the position of the centromere, which is near the middle in
some (V-shaped Y), and toward one end in others (J-shaped). The Y
chromosome has few genes in it, per unit length, and geneticists speak
of such material as "inert." Most of the chromosomes have an "inert"

segment, often very small. An inert chromosome, or segment, can afford deficiences and duplications better than others, and it seems certain that the seven variants have all sprung from one type of Y. *D. simulans* and *D. ananassae* also have variously shaped Y chromosomes.

The fungus gnat Sciara shows repeated segments of the salivary-gland chromosomes in two species. In organisms not having notably visible chromosome patterns these aberrations are hard to detect. They could
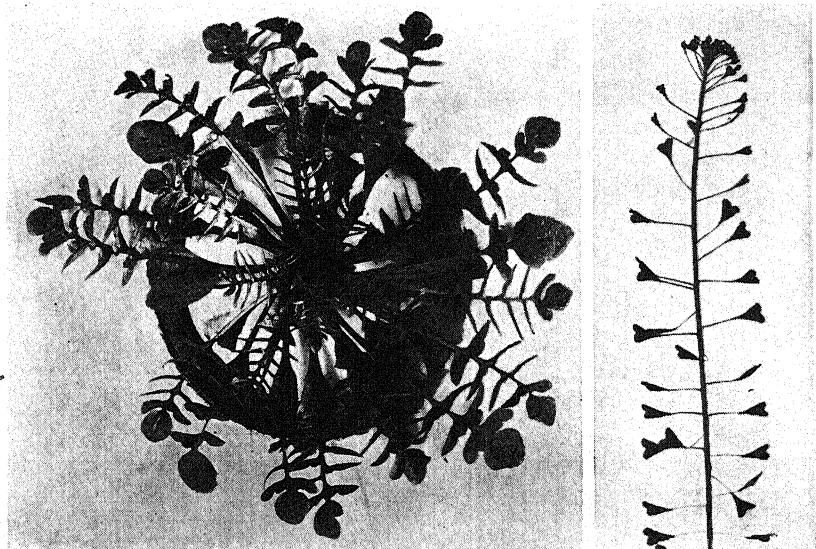
FIG. 90. Diploid shepherd's-purse, *Capsella rubella;* young plant and part of fruiting raceme. (*Courtesy of Professor George H. Shull.*)

cause unequal sizes of paired chromosomes in animals heterozygous for two chromosome structures, but unless the changes were large ones, the discrepancies could easily be overlooked.

Natural Polyploid Plants. A classical tetraploid, *Oenothera gigas* ($2n = 28$), has already been mentioned as found in the fields as well as produced in the greenhouse (Fig. 77). Another long-known tetraploid group is found in the genus Capsella, shepherd's-purse. One species was shown in Fig. 34 as an example of a wide-ranging derived species. It is known to be derived because it is tetraploid ($2n = 32$). The diploid type (Fig. 90) from which it must have sprung is represented by *Capsella rubella* ($2n = 16$), from Waco, Texas, the only known locality for this species in the North American continent. This form is believed to be ancestral to all other species of Capsella. One of the

most common of these other species, *C. bursa-pastoris*, which has 32
chromosomes, is shown in Fig. 91. Both plants there shown are dwarf,
but their small size is not caused by their tetraploidy; it results from
different mutations in the two plants.

The sundews, *Drosera longifolia* and *D. rotundifolia*, have, respec-
tively, 20 and 40 chromosomes as the 2n number; almost certainly the
latter was derived from the former. In the wheats, the numbers of
chromosomes are 14, 28, and 42, all even multiples of a basic haploid
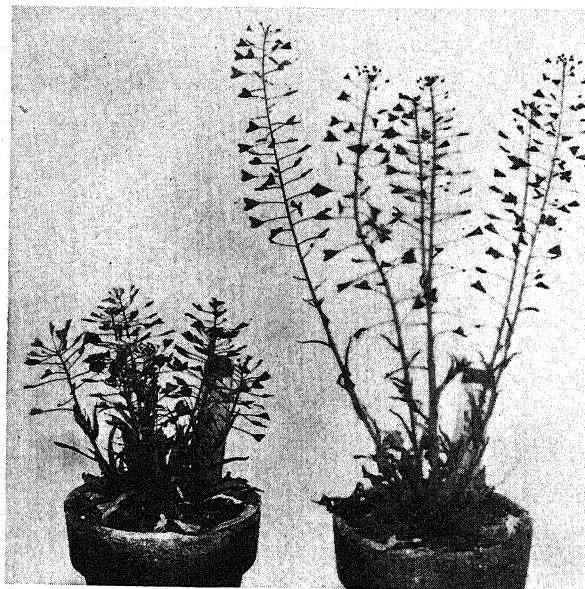
Fig. 91. Tetraploid shepherd's-purse, *Capsella bursa-pastoris*, pigmy (*left*) and
dwarf mutations. (*Courtesy of Professor George H. Shull.*)

number 7, indicating that the ancestor of the whole group had 2n = 14.
The chrysanthemum numbers are 18, 36, 54, 72, and 90; those of the
genus Solanum (potato, nightshade, eggplant, etc.) are 24, 36, 48, 60,
72, 96, and 120; poppies have 14, 28, 42, 70, 22, and 44, based on n = 7
and n = 11; sorghum has 10 or 20 chromosomes, with n = 5. Examples
of polyploidy may be found in snapdragons, strawberries, many grasses,
lilies, corn, spiderworts, nasturtiums, brambles, cotton, tobacco, rye,
chicory, docks, iris, carnations, mints, willows, sunflowers, meadow rue,
and others. Polyploidy is a common phenomenon in the flowering
plants. Stebbins estimates that about half of all species of flowering
plants have originated directly or indirectly by polyploidy. Direct

origin would mean that the species has a number of chromosomes which is an exact multiple of the basic number. However, as indicated earlier, polyploids may lose some of their chromosomes without harm because they still have enough chromosomes of the kind lost. The number 44 could come from a basic 24 by doubling, then losing 4. The species having 44 would have an indirect origin from polyploidy. In general, the high numbers of chromosomes must trace back to polyploidy at some point. Stebbins is inclined to think that, in the flowering plants, most haploid numbers higher than 10 have been attained by chromosome doubling at some time. His estimate that half the flowering plants have a polyploid origin is based partly on this assumption. These supposed derivations are widespread, not concentrated in a few groups. They are in two-thirds of all the genera—three-fourths of all the genera of grasses. Natural plant species thus indicate very strongly that polyploidy has been an important source of variability.

Auto- or Allopolyploidy? It was stated earlier that not much evolution has come from merely doubling the number of chromosomes in one plant or within a homogeneous group of plants. Such direct doubling of one homozygous diploid group of chromosomes produces what is called an *auto-tetraploid*. Sharply contrasted with

FIG. 92. Tetraploid plant of *Galax aphylla*, a species that produces autotetraploids occasionally. (*Courtesy of Professor J. T. Baldwin and Dr. Bernice W. Speese.*)

such a form is an allotetraploid, whose nature was explained in the preceding chapter. To produce an allotetraploid, two unlike chromosome groups are brought together in a hybrid and are then doubled.

There has been much disagreement as to the extent of autopolyploidy in nature. Though a Swedish cytologist had listed a considerable number of autopolyploid species, others have regarded many or even most of these as doubled hybrids, hence as allopolyploids. The hybrid need not, they hold, have been a species hybrid. Two subspecies could have

crossed, and their hybrid doubled its chromosomes. The hybrid could even have sprung from two moderately different genetic strains not of subspecific rank. The nature of allopolyploidy is thus partly a matter of definition. Stebbins allows almost any degree of difference in the parents to make their progeny a hybrid, and its doubled form an allopolyploid. Accordingly he is sure of only one real autopolyploid in nature, namely, some individuals of *Galax aphylla* (common name merely galax) from the Carolinas, Virginia, and neighboring states. Its leaves are gathered commercially for floral decoration. Typical plants have $2n = 12$ chromosomes; the tetraploid (Fig. 92) has 24. This species is the only one in its genus and has little variability; hence there is small chance for any plant to be a hybrid. Besides, the tetraploid plants differ little from the diploids in their characteristics. Interestingly enough, a single stem-tip cell has been found with 48 chromosomes, but no octoploid plants are known.

The strict definition indicated above reduces greatly the influence of autopolyploidy on evolution. It also greatly increases the amount of allopolyploidy in existence.

Allopolyploidy has another bearing on evolution besides mere multiplication of chromosomes and the change of characters dependent on this duplication. It also involves the bringing together of unlike features in the production of the hybrid in the first place. This phenomenon is accordingly discussed again in the next chapter as bearing on the general process of recombination.

Polyploid Animals. Multiple chromosome numbers in animals, as was pointed out earlier, are not common and are mostly associated with hermaphroditism or parthenogenesis. The numbers found in some species of flatworms suggest polyploidy; this is likewise true of leeches and annelid worms. These groups are all hermaphroditic. In insects, the weevils include some parthenogenetic species, nearly all of which are polyploid; all the bisexual species of this family are diploid. The four bisexual species which have been studied cytologically, and one of the parthenogenetic species, have $2n = 22$. Five of the parthenogenetic species have 33 chromosomes (triploid), and three have 44. The eggs of all the parthenogenetic species have only one division in maturation, with no reduction in chromosome number.

One species of sow bug in Europe has a diploid bisexual race ($2n = 16$) in the Mediterranean area, and a triploid parthenogenetic race (mostly females) in the north. In mountainous areas the northern triploid race extends south in France, far enough to overlap the range of the diploid, but there is probably no interbreeding. The eggs of the

triploid race undergo only one division in maturation, and the chromosome number is not reduced. Most of the other species of the same genus (Trichoniscus) of sow bugs are exclusively bisexual, and all have the same number of chromosomes as the bisexual race mentioned (2n = 16).

One species of shrimp (*Artemia salina*) also has polyploid races which are strictly parthenogenetic, along with a diploid parthenogenetic race. The bisexual race has 42 chromosomes (2n). Its eggs undergo meiosis, have 21 chromosomes, and do not develop unless fertilized. The parthenogenetic races are diploid, or tetraploid (2n = 84), or octoploid (2n = 168). All three of these types exist together at one locality in Italy. The parthenogenetic individuals produce mostly females. The eggs undergo two meiotic divisions, but the two nuclei formed by the second division fuse to form one nucleus, containing the unreduced number of chromosomes.

Another parthenogenetic crustacean, this one an ostracod, *Cypris fuscata*, with 2n = 24, must probably be regarded as triploid, since related bisexual forms all have 2n = 16.

Three combinations of ploidy and reproduction also occur in the moth Solenobia. In one species (*S. triquetrella*) a bisexual diploid race having 2n = 62, and normal meiosis in its germ cells, lives only in a small part of southern Germany. Its diploid parthenogenetic race is known from only one place near Zürich, Switzerland. The tetraploid race (2n = 124), consisting mostly of females, ranges widely through northern Europe. In both of the parthenogenetic races the eggs experience two meiotic divisions, and finish with the reduced number (31 and 62, respectively, in the two races). The first several cleavages of the egg nucleus likewise reveal only this reduced number. Then the nuclei fuse in pairs to restore the number 62 or 124. Another species of Solenobia also has a tetraploid parthenogenetic race.

In the hymenoptera (bees, ants, wasps) it is common for females to be diploid, the males haploid; females develop from fertilized eggs, while exactly the same kind of egg if not fertilized could develop parthenogenetically to produce a male. In the sawfly *Diprion simile* the 2n of females is 28, the n of the males 14, as compared with 14 and 7 in related species. White, who reports these numbers, doubts some of the other claimed instances of polyploidy in animals.

Triploid salamanders have occasionally been found, but the males are mostly sterile, so that females have to mate with the normal diploid males. From such matings have come a few tetraploids—in the laboratory, not, so far as is known, in wild populations.

Conclusion. It seems clear that the consequences of genic and chromosomal changes that happen under observation in the laboratory have their counterpart in wild populations. There is no reason to assume any other class of causes for natural variation than have been demonstrated for variation indoors. Laboratory tests and field observations furnish a harmonious group of data. Our study of evolution in nature may therefore safely use experimental results. We shall proceed on the basis of this conclusion.

RECOMBINATION

> The elementary process in a Mendelian population is change
> of gene frequency. . . . What characterizes a species is a cer-
> tain ratio of each series of allelomorphs.
> —SEWALL WRIGHT, 1933, 1931

While evolution must start with mutations of genes, reorganization within chromosomes, or alterations of chromosome numbers—the primary variation of Chap. VIII—the bulk of generation-to-generation change of organisms comes from recombination of the differing units thus provided. Part of this recombination was mentioned in Chap. VII as it relates to paternal and maternal chromosomes in meiosis. Then it was extended to the genes because crossing over prevents chromosomes from maintaining a strict individuality; genes are the units of recombination. It remains to point out the factors entering into that process, together with some of their implications for evolution in general.

Multiple Alleles. The number of ways in which paternal and maternal chromosomes may be combined was put at 2^n, where n is the number of pairs (kinds) of chromosomes. The basic number 2 is simply the number of chromosomes of one kind—maternal and paternal. Since genes are the units to be recombined, so simple an expression cannot be used unless the number of different forms of genes is the same for every locus in the chromosomes. If every gene had mutated once, and only once, and all these pairs of alternative genes were still in the population, the number of combinations would again be 2^n, in which n would be the number of loci (general kinds of genes) in the chromosomes. That condition does not exist in the animals and plants which have been much studied genetically, and it is almost inconceivable that it should ever exist in any organism.

From the complexity of protein structure, the genes, which are assumed to be protein molecules, should be subject to many different

sorts of change. Actually they have been demonstrated to change in more than one way at many different loci in a number of kinds of animals and plants. A classical instance of such different mutations of one gene is the series of forms taken on by one of the genes governing eye color, located in the X chromosome of *Drosophila melanogaster*. The first mutation of this gene to be discovered changed the eye from red to white. Subsequent mutations of this gene produced colors which have been named eosin, apricot, honey, ivory, pearl, coral, tinged, and others. At least fourteen different eye colors have been produced, in addition to the wild-type red. The 15 genes responsible for these colors are all at the same spot, the locus designated 1.5 near the left end of the X chromosome. Genes located at the same points are said to be *alleles* of, or allelic to, one another. The general meaning of this word is "alternative"; the chromosome has one or another of these genes, never more. When there are three or more forms of the gene at one locus —that is, when the gene has mutated in more than one way—these genes are collectively called *multiple alleles*.

The eye-color gene used as an illustration is not an isolated example. Genes partly governing bristles, length of legs, shape or spread of wings, form of wing veins, color of body, size and shape of eyes, and number of joints in the feet in Drosophila all have mutated in more than one way. Scores of loci in this fly have their multiple alleles. Other objects of genetic study have them. Other insects (wasps, grasshoppers, lady beetles), mammals (mice, rats, rabbits, cats, sheep, cattle, man), fish, plants (corn, evening primrose, beans, barley)—every organism studied enough to give a real chance of revealing multiple alleles has proved to have them. It is on theoretical grounds likely not only that all organisms but that all their genes have these multiple possibilities. Not all the multiple alleles may be in existence now, for mutations have a way of getting lost; but they still exist as potentialities for the future of any line of descent.

Recombination of Multiple Alleles. Each X chromosome of Drosophila has only one of the 15 genes mentioned above. Each normal female fly has only two of them in each cell, because she has two of these chromosomes; but they may be *any* two of the genes. Flies may thus be of a number of different *genotypes* (kinds of genetic constitution) with respect merely to the genes at this one locus. Let us illustrate the principle involved with only a fraction of the available genes.

We follow the geneticists in their symbols for these multiple alleles. The first mutation discovered was that to white eye, so the mutant gene was designated *w*. All the subsequent mutations were symbolized by a

basic w with a superscript. The gene for eosin eye is called w^e, that for apricot w^a, for honey w^h, for coral w^{co}, for pearl w^p, and so on. The chart (Fig. 93) ranges the genes in one of the chromosomes across the top, the same genes in the other chromosome down the left side, and the various combinations in the squares of the rest of the chart. Duplications are avoided by leaving some of the squares blank. The number of combinations into which the five alleles may enter is $5 + 4 + 3 + 2 + 1 =$

	W	W^e	W^a	W^h	W^p
W	W W	W W^e	W W^a	W W^h	W W^p
W^e		$W^e W^e$	$W^e W^a$	$W^e W^h$	$W^e W^p$
W^a			$W^a W^a$	$W^a W^h$	$W^a W^p$
W^h				$W^h W^h$	$W^h W^p$
W^p					$W^p W^p$

Fig. 93. The combinations into which five alleles for eye color in Drosophila may enter in individual flies.

15. If all 15 genes of this series were placed in such a chart, there would be 15 genotypes in the top row across, 14 in the second, and so on down to 1 at the bottom. A generalized way of formulating the total number is $\frac{1}{2}n(n+1)$, in which n is the number of alleles. Fifteen alleles produce $\frac{1}{2} \times 15 \times 16 = 120$ genotypes; 8 alleles produce $\frac{1}{2} \times 8 \times 9 = 36$ genotypes. If there has been only one mutation—two alternative genes—at a locus, the same formula is applicable; three genotypes are possible.

Recombination Involving Several Loci. The occurrence of several or many different mutations at some or all of the gene loci precludes any

simple formula for the number of combinations, like 2^n for maternal and paternal chromosomes. The computation is more complicated. It is not likely that most of the genes in a population would have mutated the same number of times, but some of them certainly would. Suppose that 6 genes had mutated 7 times each; there would be 8 different genes at each of the 6 loci. For one such locus, the number of genotypes would be 36 (see preceding section). For all 6 of the loci, the
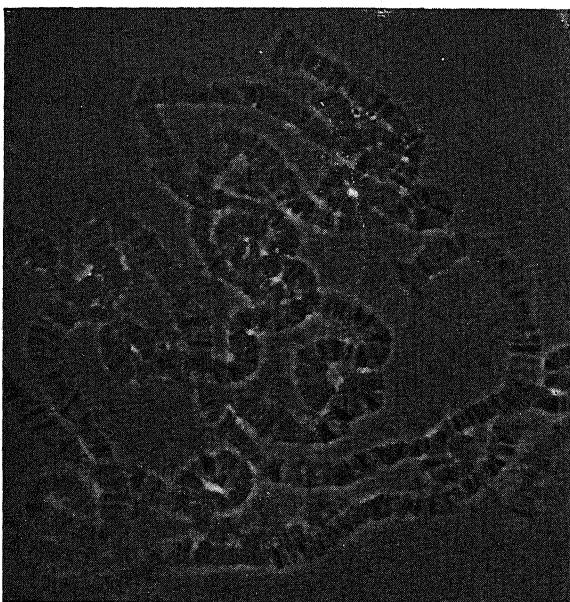
Fig. 94. Phase-microscope photograph of unstained salivary-gland chromosomes of Drosophila. (*The Research Division, American Optical Company, Stamford, Conn.*)

number of combinations would be 36^6. Suppose that in addition there were 5 genes at each of 9 other loci. That would yield 15 genotypes at one locus, and 15^9 for all 9 loci. Combining the first 6 loci with the second 9, there would be $36^6 \times 15^9$ combinations. For each group of loci at which there were the same number of mutations, the number of possible genotypes for those loci would be another multiplier in the product which has been merely begun above.

Total Number of Genes. How far the multiplication of genotypes may conceivably go depends in part on how many genes there are. In no animal or plant can the genes be counted. They probably cannot be seen. The only place where any one has recently suggested that genes

can be seen is in the salivary-gland chromosomes of flies (Fig. 94) and
their relatives, and the number of visible bands across these chro-
mosomes is too small for the number of genes which other kinds of
evidence indicate. There *was* a time when the little knots on threadlike
chromosomes, particularly those of plants, were thought to be possibly
the genes, but again there are too few of them to fit other evidence.
These knots may have no relation at all to the genes.

Various ways of estimating the total number of genes have been
used. Some of them can be indicated here but only in a general way.
One of the earliest estimates for Drosophila rested on the frequency of
repeated mutations of the same gene. On the assumption that all genes
mutate with equal readiness, the fewer the genes the more frequently
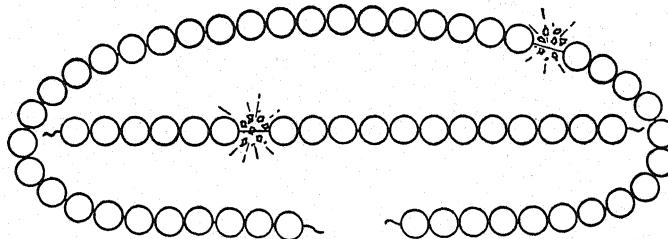
FIG. 95. Strings of beads which are randomly broken one at a time, illustrating a
method of counting genes by means of repeated mutations.

will the same gene mutate, in a given total number of mutations. As
a crude illustration of the principle involved, suppose that a string of
19 beads (Fig. 95) is subject to some sort of bombardment which breaks
one bead at random. The bombardment is repeated many times and
a record kept of which bead is broken each time. After 19 breakages
there *must* be repetitions, and long before that time there *would* have
been repetitions. In a hundred breakages there would be expected a
certain amount of such repetition. As a contrast, let the same experi-
ment be performed with 45 beads, one of which is broken at each
bombardment. In a hundred breakages the repetitions should be much
fewer. The fewer the beads, the more repeated breakages there would
be. Finally, suppose the number of beads is not known, but that in such
an experiment the extent of repetition of breakages has been ascer-
tained among a total of, say, a hundred breakages. From these data
the probable number of beads can be computed—the fewer the repe-
titions, the more beads there must have been.

Substituting genes for beads, and mutations for breakages, and rea-
soning backwards, one may say that the more often some particular

genes mutate, within a given total, the smaller the total number of
genes must be. The haploid number of genes was first estimated for
Drosophila by this method as about 1950. This method is vitiated by
any proneness of certain genes to mutate frequently. It is thought that
the eye-color gene which has mutated 14 ways, and a number of times
in the same way, is an especially mutable gene. A much more extreme
instance of a mutable gene. occurs in another species of Drosophila,
in which the mutant gene "miniature" in certain stocks returns very
frequently to the wild type. The effect of any tendency to mutate often
is to make the computed number of genes too small. Other ways of
computing the number indicate that 1950 *is* too small.

Another method of estimating the number of genes is by comparing
the distance between genes with the length of the chromosomes. The
distance between genes is measured by the amount of crossing over
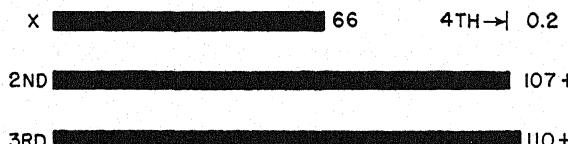
FIG. 96. Chromosome map lengths in Drosophila, in terms of crossover units.

between them. The length of the chromosomes is the sum of all the
small distances between specified genes as determined by crossing
over. Now, the total length of the chromosomes in Drosophila is about
284 "units" (Fig. 96), and the nearest neighbors among the genes are
about 0.1 of one of these units apart. If all adjoining genes are the same
distance apart, that would mean 2840 genes—again the haploid num-
ber.

Radiation experiments in the production of mutations have furnished
another method of estimating numbers of genes. It is assumed that a
gene mutates when it is traversed by one of the particles, and the aver-
age distance between the paths of particles is governed by the dosage.
Genes would have to be of a certain size to be hit a specific number
of times by rays a given distance apart (Fig. 97). The volume of
chromatin divided by the gene size thus ascertained affords a num-
ber of genes. Gene sizes in *Drosophila melanogaster* have been esti-
mated at 4 to 8 mμ in diameter (if spherical), and the number of them
in the X chromosome at 280 to 840. If the autosomes have numbers of
genes proportional to their size, the total number should be about four
times those named. Another estimate from radiation work puts the

number in the X chromosome at 1860. For *D. pseudoobscura* a comparable calculation for the third chromosome (the one with so many inversions) indicates that it contains not fewer than 289 genes capable of mutating to a lethal form, and probably not over a thousand.

One may compare with these figures the loci that are known to have mutated in *D. melanogaster*. A compilation of all the genes whose mutations have been located by crossover tests includes, according to a count of them by Dobzhansky, 537 loci. The number discovered and located by geneticists, even in as thoroughly studied an animal as Drosophila, can scarcely be more than a modest fraction of those that have occurred. Those who have occasion to mention the probable number of genes in animals have shown a tendency to assume 5 or 6 thousand pairs in body cells, though some have postulated numbers much higher. For example, one estimate of the genes in man places the haploid number at 20,000 to 42,000.

FIG. 97. Principle of measuring the size of a gene in relation to its prospect of mutating as a result of irradiation.

Any of these numbers, even the smallest of them, if used in the computations of recombinations made in the preceding section, would lead to stupendous numbers of different possible genotypes. If there are 5000 loci, and the gene at each one existed in 6 allelic forms, the number of possible genotypes would be 21^{5000}. Even if only a quarter of the genes ever mutated, and even if these mutated only once or twice for each locus, the number of genotypes would be beyond human comprehension. With such potentialities evolution by recombination could continue for a very long time.

Stability *versus* Variability. A species which could contemplate its own prospective evolution might well regard its opportunities for change through recombination as frighteningly large. Evolution could under certain circumstances be too rapid for the good of the species experiencing it. The danger of too great speed is in relation to the environment. Most organisms are rather well fitted to their environment —a fact that needs to be pointed out here, though the reasons for it belong to another chapter. Some evolutionists say that at any one moment a species is about as well fitted to the environment as its own variability permits it to be. That may be an overstatement, but it is nearly enough true to serve as the basis of an argument. So long as the

environment remains as it is, a species perfectly fitted to it would do well not to change. Recombination results in many individuals less well fitted; the more recombination there is, the greater the wastage. If recombination were so extensive as to leave very few individuals like their well-fitted parents, the species might even be in danger of extinction in stable surroundings. Enough individuals of the right kind must be produced to hold their niche in the environment.

If a population should, either in response to the stability around it or for quite different reasons, lose its variability and then the environment did change, it would again be in danger but from another direction. The extent of the danger would depend on the degree of change in surrounding conditions. The variability of a species should, to be most useful, be conditioned to the variability of the environment. As baldly stated in the preceding section, the possibilities of change through recombination might seem to outstrip any likely change of environment.

Brakes upon Recombination. Living things have, in their evolution, met the outlined situation by changes in their own organization. Presumably in the early stages of life on earth organisms were much simpler than now. Many biologists have suggested that something corresponding to modern genes—the ancestors of those genes—were once independent organisms. More than one geneticist has likened them to viruses, which also reproduce with fidelity and are of very small size (Fig. 76), though it has been suggested by others that viruses may have degenerated from a more highly organized state rather than being on their way to something more complex.

If those early organisms came to associate themselves with others in some sort of living envelope, but remained quite independent of one another in that envelope, the dangers of too rapid recombination could exist to the full. Collecting the organisms (genes) into several groups (chromosomes) would have checked the recombination to whatever degree the chromosomes possessed stability. If chromosomes restricted reassortment of genes too much, reorganization of them could remove part of the limitations.

The recombination referred to so far would have been of the irregular type involved in asexual reproduction—assuming that early asexual reproduction permitted reassortment. This would have been a wasteful method. Introduction of sexual reproduction, with meiosis, would have provided regularized variation, the extent of which would be governed by the amount of crossing over.

It is more than likely that the evolutionary process just outlined is not what actually happened. But it seems necessary to suppose that

living things have had some way of balancing change against permanence. They would hardly have succeeded as they have done without the possibility of adjusting themselves to a slowly changing environment and at the same time avoiding the wastage of changing too fast.

Another brake upon recombination is found in certain chromosome reorganizations. Inversion heterozygotes show a restriction in crossing over in the chromosome pair that has the inversion. Curly wing (Fig. 98) in Drosophila is associated with an inversion in the second chromosome. These chromosomes pair fairly well in the salivary glands by means of a loop, after the manner of Fig. 88, and may pair equally well in the oöcytes. But for some reason there is almost no crossing over in that pair. On occasion the noncrossover effect is largely lost, and genes in the second chromosome with curly in the homologue cross over rather freely; but the change is only temporary. All curly-winged flies are heterozygotes, since curly is lethal in homozygotes, Translocation heterozygotes also have less crossing over because the chromosomes do not pair properly.

FIG. 98. Curly-wing mutation in Drosophila, which is associated with an inversion for which the flies are always heterozygous. (*From Ward, in Genetics.*)

Sex-linked genes, over a series of generations, cross over less frequently than do autosomal genes, because one of the sexes has only one of the chromosomes that contain them (X in mammals and most insects). There can be no crossing over in this chromosome when it has no homologue. In Drosophila, the prohibition extends to autosomes as well, for there is no crossing over at all in males. In neither instance is the prevention of crossing over a character of the chromosome itself. These chromosomes pass from one sex to the other in successive generations, and in the sex that has two of them there is the usual amount of crossing over. For the species, however, recombination of sex-linked genes is less than that of autosomal ones.

Reservoir of Variability. The possibilities of recombination presented in the preceding sections may seem to indicate more extensive use of trial and error in evolution than is actually practiced. At no time are the different forms of the gene at a locus as numerous as they conceivably could be. Possibly each of the forms to which a gene could

mutate may have existed at one time or another in the ancestral line, but they do not all exist now. Indeed, so far as can be ascertained, relatively few of them are present at any moment. Mutations are mostly lost. A gene that survives does so by being in an individual that survives, and most individuals do not succeed. Most species produce, as fertilized eggs, many times as many offspring as can attain maturity and in turn leave offspring. A mutant gene, to persist, must be in one of the few individuals that live to produce offspring, and only occasionally does a gene that is as rare as a new mutation must be have that good fortune. If it passes its first test, it has to meet another, perhaps just as severe, in the next generation. Luck must be continuous. If the new gene is lost, another just like it may sometime be formed by a repetition of the same change. That helps, but the gantlet to be run is no less trying than the first one. Some mutant genes, to change the figure, do pass through all the successive screens which strain them; that is why there is any variation at all in a population; but the variability is much less than a recital of the numerous opportunities might lead one to suppose.

Enough mutations are preserved in most populations to provide a considerable reservoir of variation on which evolution may regularly draw. The numerous instances of alternative genes in wild populations which were mentioned in Chap. IX are all part of this reservoir, and every species must have this source of change in some degree. Mutation, including repetition of old mutations, adds to the store, but there are factors working in the opposite direction. The balance resulting from the interplay of these opposing forces determines how well a species is fitted to vary as the environment makes such variation necessary.

Random Loss of Variability. One of the forces reducing variability, long overlooked, may seem to be plain arithmetic, but it involves a fundamental biological phenomenon. This force is the tendency of a gene that is in a minority among the alleles at its locus to become a smaller and smaller minority over a series of generations. A gene that is in only one-tenth of the pertinent chromosomes now is likely to be in only one-twentieth of them much later. The smaller the proportion it is in now, the more rapidly should its representation decline in the future.

The frequency of an allele (the percentage of the chromosomes it is in) fluctuates from generation to generation. This fluctuation follows from the randomness of meiotic divisions, of fertilizations, and of survivals among offspring. If a gene's representation drops in one generation, it may well rise an equal, or even greater, amount the next

generation. That is, its representation *may* rise *if* there are still any individuals left that contain the gene; for genes come only from genes by reproduction. If a gene is in only a small number of the pertinent chromosomes, those chromosomes may, in their area, all be in individuals that perish. After that there can be no upward fluctuation of the rare gene's frequency. It is lost from that population. The gene may be present elsewhere in the range of the species, but in this particular breeding area it is lost—barring a repetition of the mutation or immigration from other areas. The fluctuation of genes is thus different from fluctuations not involving reproduction. The income of a corporation may fluctuate upwards from nothing; there may be income one year even though there was a loss the year before. Income is not reproduced from income, it is derived from capital, labor, ideas, and demand. Even some biological phenomena fluctuate upward from nothing. There may be many winged aphids this generation, even though all were wingless the generation before. This is true because wings are not reproduced from wings; they depend on the length of the periods of darkness to which the aphids are exposed. But genes come only from genes, and a gene once lost is lost forever from its population, except for replacements.

A gene that is present in 10 per cent of the chromosomes would seem to be safe, because fluctuation in one generation would hardly be so great as to remove it completely. But distribution is never uniform. If the gene's representation is 10 per cent in the species as a whole, there would be areas in which it was in only a small fraction of 1 per cent of the chromosomes. In these areas it could be lost entirely, and with only the usual amount of migration it could not be restored in them. The net result of such local losses would be a small loss for the species as a whole. Repetition of local losses should continue until, in time, the gene would disappear from all areas.

The gradual loss of minority genes, with the corresponding fixation (complete homozygosis) of their alternative alleles, tends to lower the reservoir of variability. Some evolutionists have spoken of this change as the "decay" of variability. It is a process to which populations in general are subject—except as other phenomena are in opposition.

Size of Population. Most generalizations have to be qualified, and the one just stated concerning reduction of variability is no exception. The rate of reduction, even its extent, depends on the size of the population. In appraising this qualification, one must understand what the population is. It is the group of individuals which freely breed with one another. Almost never could a whole species be one such population;

only an extremely localized species, perhaps a young one which had never yet been recognized as distinct from others, would have any chance of being a single population in the evolutionary sense. Moreover, the population is a different one for every individual. In a general way, each animal is in the center of a circle which contains its breeding population. Even within this circle the terms of the definition are not quite met, since usually those near the periphery of the group do not breed quite so freely with those at the center as those at the center do among themselves. Breeding population is a concept rather than an actual group. For purposes of computing the opportunities of evolution, the breeding population must deliberately be made a concept
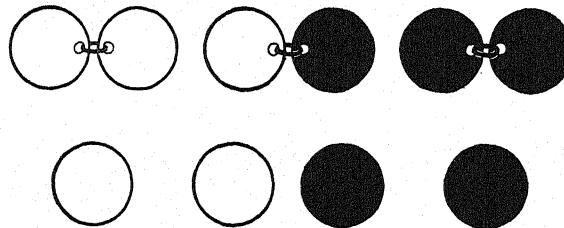
FIG. 99. Poker chips of two colors used to demonstrate random loss of variability. Tied together, they represent genotypes; singly, the germ cells. Random matings and random fertilizations lead eventually to loss of one of the genes.

that does not coincide with a concrete assemblage. For example, if the size of the group fluctuates greatly, as it often does seasonally, the "size of population" as it enters formulas must be nearer to its minimum size than to its maximum. Likewise, if the sexes are not about equally numerous, "size of population" must be taken as less than the actual number of individuals in it. Size of population is thus an idealized number which, when fed into a formula, leads to a correct judgment about recombination in evolution.

The formulas referred to have been derived mathematically, largely by Wright, and the derivation is quite beyond the scope of this book. Even the conclusions to be derived from Wright's formulas are not as a rule easily stated. One that is easily understood is to the effect that loss of variability, of the kind discussed in the preceding section, is especially marked in small populations. The effect can be demonstrated in laboratory exercises, where symbols represent genes (Fig. 99). A dozen adults are paired at random, and their germ cells are combined at random. Of two alleles, equally numerous at first, one usually disappears—in perhaps twenty or thirty "generations." Sometimes only gene

A is left, sometimes only *a*. A small population thus tends to become fixed, that is, completely homozygous, a state which ends evolution by recombination until other mutations occur. In a very large population, on the contrary, the change of frequency of a minority gene is negligible. While alternative genes combine freely, they retain about the same frequency; that is, there is little evolution by recombination. A much better opportunity for evolution by recombination is afforded by populations of intermediate size. Probably the best chance for recombination is in a rather large population more or less broken up into local areas in which the frequencies of allelic genes are different.

Migration. If the small groups into which a large population is divided are *completely* isolated—meaning merely that they do not intermingle—each group tends to lose its variability as one allele at each locus comes accidentally to be the only one preserved. Such isolation, however, is probably seldom actual; there are nearly always individuals passing from one small group to another. The effect of this migration is to increase the conceptual "size of population" and to increase variability. How well the variability is maintained or how much it is increased depends on the extent of the migration. Wright has computed the results of different degrees of wandering, though no formula can precisely fit any specific situation. If the migration could bring about an exchange between each small group and *all* the others, an exchange of only one individual every second generation would be a sort of zero value marking the line between random fixation of genes and maintenance of variability. Migration more frequent than that would prevent, migration less frequent would permit, fixation of alleles—one allele in some groups, another allele in other groups.

Actually the migration cannot involve all the small populations equally; it must be from each group to its neighbors in very different amounts. Under these circumstances much greater dispersal than one individual every second generation would still enable one allele to become fixed in one population, another allele fixed in another small group. Nevertheless, the influence of migration is in general toward maintenance of variability.

How Large Is a Population? How many individuals do actually meet in such a way that they could be regarded as a breeding population? The answer obviously depends on the characteristics of the animals in question. A favorably situated insect species could have large breeding populations; mice in a meadow, in an average season, would presumably exist only in small populations. Some attempts have been made to compute population sizes from some of the consequences of

that size. Recessive lethal mutations in Drosophila furnish a means of attacking this problem. The lethal genes in a species may mostly be at different loci in the chromosomes (nonhomologous), or they may include many at the same loci (homologous genes). More flies would be killed in the latter situation than in the former, since only a fly homozygous for one recessive lethal would be destroyed by it. Now, the lethals in one breeding population are more likely to be homologous since some of them may be descendants of an original mutation. Lethal genes arising in different populations are less likely to be homologous. The details of the mathematical argument cannot be indicated here; it is merely pointed out that lethal genes afford a way of estimating the size of a breeding population. One study in Death Valley indicated that the breeding populations of *Drosophila pseudoobscura* were less than 2500, perhaps much less.

For larger animals, and especially those which do not travel extensively, populations must be much smaller. Exact figures are not available. There are many records from ecological and taxonomic work of species that are divided into numerous separate colonies between which there can hardly be any exchange. A breeding population in one of these could not be greater than the total number of individuals in that area, but it could be less. Seldom is there any reliable information about even the total number of individuals present, since censuses, even if they could have been taken, were not on the program of the studies that revealed the separation of the colonies. It is obvious from them, however, that breeding populations may be quite small.

Territoriality and Population Size. Among vertebrate animals high enough in the scale to have certain individualistic psychological properties, there is a rather widespread phenomenon which tends to reduce the effective size of populations. It is known as territoriality. It has been much studied in birds, less extensively in small mammals, still less in lizards. By the uninitiated it might be supposed that birds, with their powers of locomotion and their habit of migration, might constitute large populations. They do not, however, migrate at the breeding season, and that is the only time at which size of population is significant in relation to recombination of genes in evolution. It is, indeed, the only time at which there is a breeding population. At the breeding season it is the practice in many species for an individual male to take over an area in which he assumes squatter sovereignty. This area may be several hundred meters across. From this area the self-appointed proprietor undertakes to exclude any others of the same species and same sex. Sometimes those of certain other species are like-

wise excluded; perhaps in these instances the different species are more nearly competitors than other species usually are. Small mammals also maintain their pre-eminence in areas of their choice. Most vertebrate animals limit their activities to a small area—two or three acres for a mouse—but that area is hardly to be called territory unless they defend it. Fights occur in maintaining supremacy, and sometimes "property" changes hands.

The general effect of territoriality is to reduce the number of individuals which may meet, and so reduce the population size.

Population Size in Man. The size of human populations varies tremendously. In primitive peoples, with little means of transport, the breeding unit is necessarily small. In civilized countries, with travel prevalent, it should be much larger. In all peoples, taboos, social classification, differences in interests all tend to reduce it. In towns the population unit is larger than in rural areas, even with prevalence of automobiles on the farm. College towns, with their shifting human content, presumably have larger populations than other communities of equal size.

Some actual figures for population size may be derived from studies by Dahlberg on inbreeding in man. He was interested in inbreeding as a question of eugenics, but his formulas can be worked backwards. Part of his argument relates to the frequency of cousin marriages. If such consanguineous matings are arranged at random, they should be more frequent in small breeding populations than in large ones. Support for this thesis is found in the fact that cousin marriages are more common in small towns than in large ones. While the whole town is not a single breeding population as a rule, a city offers more opportunity for large breeding populations than medium or small towns do. Now, the frequency of cousin marriages in certain places at specified times has been obtained from various studies. Using these frequencies Dahlberg could compute, for example, that the average size of the breeding population in Bavaria in the latter half of the nineteenth century was around 500, while 50 years later it had risen to nearly 2000. This increase was to be expected from increasing density of population and improving means of travel.

Secondary Results of Recombination. So long as genetic units are transmitted without change in their expression, recombination of them gives only predictable results. Various eye colors, the different shapes of wing, the several colors of body in Drosophila can be combined in the imagination in ways that may be precisely verified by making all the necessary crosses. Sometimes, however, the results of recombina-

tion are genuine surprises. Genes at different loci interact, and the products of their combined action would never have been guessed in advance. This is naturally more often true if the genes at different loci affect the same part of the organization—both or all of them eye colors, both wing shapes, etc. Beginning with the early-discovered walnut comb of fowls out of the combination of rose and pea combs, and the surprising production of colored sweet peas from a combination of two white ones (Fig. 100), hundreds of examples of interacting nonhomolo-

FIG. 100. Color in sweet pea produced by interaction of chromogen of one white parent with enzyme of the other white parent.

gous genes have been put on record. They furnish many of the exercises in all moderately elementary studies of heredity.

What happens in the physiology of development of the visible characters is not usually known. It is a well-defined current theory that each gene locus is responsible for one biochemical synthesis—for the production of one enzyme. Mutation of a gene prevents the formation of its specific enzyme, or changes it to a different enzyme. What the result of combining two new enzymes would be could hardly be anticipated. The possibilities of combined action are brought forward here as part of the phenomenon of recombination, but they have a more direct relation to a later topic. Mutations happen only occasionally, by ordinary standards, and two genes whose enzymes might interact in some specific way are not likely to arise simultaneously. One mutation occurs, let us suppose, and nothing is observed to happen. Another gene mutates, perhaps in another breeding population, and again nothing appears to be changed. More likely both mutations produce physiological modifications that are not detected. Then perhaps through

repeated mutation in one of the populations the two mutant genes are brought together, an interaction results, and some new character is produced. The new product may be physiologically important, even if not detected.

The new character would not be regarded as a recombination product; it would seem to be the product of one mutation. Yet one of the genes has been present a long time—in a sense waiting for its collaborating gene to come into being. Most discoveries of evolutionary steps must be of this kind. Interactions are probably universal. This situation needs to be kept in mind in considering the guidance of evolution in another chapter.

Recombination a Stimulus to Primary Variation. Since some mutation is gene-controlled, it is not surprising to find that the bringing together of two groups of genes in hybridization sometimes increases the mutation rate. The hybrids produced by *Drosophila pseudoobscura* and *D. persimilis* show a strikingly higher mutation rate than pertains to the same genes in the parent species. A smaller increase is shown in the hybrids of *D. melanogaster* and *D. simulans*. Whatever genes cause greater mutation apparently affect the genes of another species more than those of their own. Practical breeders have often claimed greater variability because of domestication, but this could be a result of the hybridization to which domestic animals and plants are subject.

This particular effect may not be common, but to whatever extent it occurs it savors of fire feeding on fire—recombination leading to greater variety of genes from which still more recombination may result.

Hybridization of Plant Species. Though there is considerable limitation on the crossing of species—that is one of the things that make them different species—such crossing does occur, chiefly in plants. When crossing occurs freely, and the hybrids are fertile, subsequent hybrid generations segregate out into numerous combinations. Extreme instances are some—not all—of the crosses between species of snapdragons, genus Antirrhinum. The crosses referred to produce hybrids that are about as variable as the more variable of the two parent species. When these are inbred, the F_2 generation is exceedingly variable; hundreds of different kinds occur. The crossed species must differ in many respects, and there is free recombination of the contrasted characters. Some of the observable characters of the F_2 hybrids are not found in either of the parent species—an example of the interaction of genes recently mentioned. The freedom of this recombination must

indicate close homology of the chromosomes of the two species, and regular pairing of them in the hybrids. The fertility of the hybrids and preservation of so many combinations of characters must rest on such homology.

Most species hybrids do not enjoy the fertility and free recombination described above; they leave reduced numbers of offspring, if any at all, and certain combinations are more likely to survive than are others. Lowered homology of the chromosomes of the two species is the primary cause of this restriction. Yet, so long as hybrid offspring are produced, and they have any degree of fertility, there is opportunity for recombination through species hybridization.

Most of this recombination through hybrids of plant species involves allopolyploidy. As we have seen, a large share of the species of flowering plants have had a direct or indirect origin through polyploidy, and in the judgment of Stebbins most of these origins come from allopolyploidy—crosses of plants having unlike chromosome complements plus the doubling of all chromosomes in the hybrid. Were allopolyploidy to lead to the pairing *only* of the sister chromosomes produced by the doubling, hybridization would lead to a combination of the character of both species, but to little more *recombination* thereafter than might occur within either species. However, there is often enough homology *between* the species to cause irregularities in the pairing of the chromosomes, leading to variant germ cells, hence to recombination, much or most of it inviable.

Among the species crosses that have led to recombination are those between different tobaccos, both in greenhouses and in nature; among species of cotton, again in nature as well as at experiment stations; and a number of times in chicory, wheat, lilies, strawberries, gourds, and other plants. In lettuce, several species have n = 17 chromosomes, and these cross to produce fertile hybrids; but some species with n = 9 do not cross. More than chromosome number is involved in species hybridization. One lettuce species with n = 17 may be crossed with another with n = 9, to produce a hybrid with n = 26; but the species characters in this hybrid do not segregate—there is no recombination. Two birch species have been crossed, with segregation in their hybrid. Species of Solanum (potato-nightshade-bittersweet group) cross if their chromosome numbers are the same, and recombination follows. Species of brome grasses, all with 2n = 42 chromosomes, have been crossed, with the expected low fertility of the F_1. From the F_1 some diploid F_2 plants were obtained, in which there was recombination of the species distinctions. Colchicine treatment of F_1 yielded a tetraploid

F_2 which, as an allotetraploid, might well not have shown any recombination if pairing at meiosis were always between sister chromosomes produced at the colchicine duplication. There was, however, about as much recombination in the allotetraploid as in the diploid F_2. This presumably means that there was considerable homology between the chromosomes of the different species, so that in their hybrids all four chromosomes of a kind joined at meiosis, with resulting variability of the chromosome content of the germ cells. In general, allotetraploids have either high fertility and low recombination, or low fertility and high recombination; it all depends on the degree of homology between the chromosomes of the crossed species.

Even generic crosses are possible, and some of them yield variability. This is true of Triticum (wheats) crossed with Agropyron (wheat grasses); their hybrid initiates considerable recombination.

Species Hybrids in Animals. Less success attends the crossing of animal species as a step toward recombination. One example of supposed species hybridization in Drosophila is the origin of D. *americana* from a hybrid of D. *novamexicana* in central Texas, whence the new type migrated up the Mississippi Valley. One ornithologist reports a cross between two species of sparrow (*Passer domesticus* and *P. hispaniolensis*) in north Africa, but there is little variability (recombination) in the hybrid. What are believed to be hybrids of the blue-winged and golden-winged warbler show several combinations of the distinguishing characters of the parent species. Two foxes of different genera, *Vulpes vulpes* (red fox) and *Alopex lagopus* (arctic fox) can be crossed, but the hybrid is sterile. Two genera of fishes can likewise be crossed in aquaria (*Platypoecilus maculatus* and *Xiphophorus hellerii*), but in nature they do not live together; the former lives in the lower courses of streams, the latter in the headwaters. Crosses among pearl-neck, Senegal, and ringdoves are made in laboratories, and antigens in the red blood cells are reassorted. Since some of the species differences relate to these antigens, there could be some evolution from such crosses. In general, it seems certain that little animal evolution has come from hybridization of species. Recombination in animals has to start at lower levels—mostly no higher than races.

Anastomosing Lines of Descent. In view of the occurrence of species hybridization in plants, it is needful to point out the effect this has on lines of descent. In relating classification to evolution, use was made of a treelike diagram in Fig. 17, in which orders were divided into families, families into genera, and so on. The branching nature of the classification was shown to be what evolution of taxonomic distinctions

would require. For groups in which species do not cross (most animals), that is a fair picture of their kinships. Species that have similar genes must have maintained that similarity over the generations since their common ancestry. Any considerable similarity would mean either little mutation, or similar mutation, in the separate lines of descent. For the most part, genes that go into different animal species have parted company for good; only parallel evolution, or lack of evolution, could keep them alike thereafter.

In plants, where species cross, genes may part company in different species, then come back together in a species hybrid. Through this hybrid they may, by later crosses, join other genes (or their descendants) from which they had separated much earlier. Lines of descent of genes may thus cross the boundaries of taxonomic groups in a very irregular fashion. Such descent of genes may be likened to anastomosis of blood vessels; a vessel branches into a number of parts, these parts may join one another, and the vessels formed by their union separate again into branches. A complex network of vessels results. Descent of genes, in the presence of species hybridization, may form such a network; but when species do not cross, the branching diagram fairly represents the interrelationships of genes.

GUIDANCE OF EVOLUTION

There is no theoretical necessity for supposing that evolution has proceeded in the same way in all groups. In some it may proceed largely under direct selection pressure following change of conditions, in other cases it may be determined by random differentiation of small local populations, with or without inter-group selection. It may even be dominated by mutation pressure in special cases. It may be a gradual, fine-grained process or at times a coarse-grained process, new species arising directly from hybridization and polyploidy.

—SEWALL WRIGHT, 1940

The large amount of potential mutation of genes, of reconstruction of chromosomes, and of possible recombination of these primary changes is far in excess of the variability that has ever yet been realized in living things. There are many conceivable types of beings that do not exist and never have existed. Some are known to have existed once and become extinct, and presumably many have been extinguished without leaving any record. Yet after allowance is made for these unknowables, it seems clear that many conceivable products of evolution still await realization. Something has had to decide which of many courses supposedly open should be followed. A number of factors of guidance are known, and some conclusions reached as to the part which each one plays.

Mutations of Limited Kinds. A first step in circumscribing the course which evolution may take is the strict limitation placed upon the nature of mutations. In so far as these gene alterations furnish the primary changes for evolution, no change of species can go in directions for which there are no appropriate mutations. Certain discussions of evolution have been based on the assumption that mutations of every conceivable kind not only may be but are produced. Were this true, evolution *could* go in every conceivable direction. If it is not true, evolution is limited to those directions which mutation throws open.

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There are a number of indications that the nature of mutations is limited. The structure of the gene, if it is a protein molecule, should permit modifications only in certain ways. These ways should be numerous, but not of infinite variety. The more or less stable units making up the molecule resist alteration, while the bonds that connect them at least permit substitution. Randomness of mutation would thus not be expected.

Several phenomena indicate positively that the changes of genes are not random. One is that mutations, in situations where a scale of possibilities exists, do not actually realize all those possibilities. Eye color in Drosophila should, if every change which is conceivable is also possible, mutate to any color in the spectrum. Actually, aside from white, the colors are all in the red range, none green or blue. Some other insects have green eyes; hence the absence of green in Drosophila must mean that mutations which would result in that color are impossible.

Parallel Mutation and Variation. Parallel mutation in laboratory animals and parallel variation in nature must also mean a limitation on the kinds of mutations. Two species of flies in the laboratory have produced identical mutations quite independently of one another. Both *Drosophila melanogaster* and *D. simulans* have experienced mutations of eye color to prune, ruby, and garnet; of body color to yellow; of bristle shapes to forked and bobbed; and of wings to crossveinless, vesiculated, and rudimentary. That these mutations actually are identical is proved by crossing corresponding mutants of the two species and getting the same mutant phenotype in the offspring; if the parental mutations were not homologous, the offspring would be of wild type. These mutations cannot arise in one species and be transferred to the other by crosses for, while the cross can be made, the hybrids are sterile. The identical mutations arose independently. So many similar changes could not have been produced at random; something must direct mutation in particular channels.

With this proved example of parallel mutation at hand, instances of parallel variation in species that cannot be crossed must presumably be explained the same way. Ruby eyes with dilute fur color has appeared in mice, rats, rabbits, and guinea pigs. A recessive yellow fur color has arisen in three of these rodents, pink eyes with dilute fur color in three of them, brown agouti in three, a dominant black in two, and white fur with colored eyes in two. If variation were random, such equivalence could hardly exist. While homology of the mutations cannot be proved without crossing, it presumably exists.

Recurrent and Reverse Mutation. Repetition of the same mutation, which has often happened in genetically well-known organisms, and reverse mutation back to wild type, also indicate that change is guided. In X-ray experiments with Drosophila, the same mutation turns up again and again—garnet eye in 1 chromosome in 4000, forked, ruby, yellow, and white 1 in 8000, cut wing, singed, vermilion, carmine, and prune 1 in 22,000, and others. At the white-eye locus, while white mutates to the other allelles with about equal frequency, those other alleles mutate to white about three times as often as to one another. Among induced mutations in bacteria in one group of experiments, 27 changes destroying the capacity to synthesize tryptophane were all probably the same mutation.

With all conceivable changes open to them, the chance that genes would do the same thing a number of times or repeatedly undo what they have done must be considered negligible. The alternative possibility, and the one that must be regarded as probable, is that mutation is directed. Recurrent mutation is considered again later, not merely as proof that evolution is limited to certain channels, but as a positive factor promoting evolution along a given course.

Gene Frequency. The further steps which lead to the change known as evolution involve increase or decrease in the frequency of alternative genes at the various chromosomal loci. If gene A has only one mutant form a, which has spread to 10 per cent of the chromosomes of the population that carry that locus, the frequency of gene A is 0.9, that of a is 0.1. If something happens to increase a to 11 per cent, reducing A to 89 per cent, that change in the frequencies is evolution. Now, frequencies of genes are determined by the frequencies of the individuals containing them. A gene is lost when individuals containing it are lost; it increases in frequency when more individuals possess it. The individuals possessing the locus of A and a are of three kinds, AA, Aa, and aa. Whether these three kinds of individuals are all different in phenotype or otherwise detectable respects depends on dominance. If one of the alternative genes is dominant over the other, there are only two recognizable kinds of individuals; if A is dominant, AA and Aa are alike. If neither gene is dominant, Aa is distinguishable from the other two, and there are three recognizable kinds of individuals.

In accordance with what is called the Hardy-Weinberg principle, if the frequencies of genes A and a in a large population are 0.9 and 0.1, respectively, the population should consist of 81 per cent AA individuals, 18 per cent Aa, and 1 per cent aa. This conclusion is arrived at on the theory of chance. The germ cells should be of two kinds, A and

a, in the same fractions as are the genes. If one figuratively reaches into the supply of eggs and draws one out at random, the chance that the one drawn is an *A* egg is 0.9. A sperm similarly drawn at random from the supply has also a 0.9 chance of being *A*. Thus the chance that a fertilized egg (hence an individual of the next generation) will be *AA* is 0.9 × 0.9, or 0.81. The expected frequencies of the three kinds of individuals may be computed in one operation by merely squaring the binomial 0.9 *A* + 0.1 *a*. The result is 0.81 *AA* + 0.18 *Aa* + 0.01 *aa*. This product may be generalized as $p^2AA + 2p(1 - p)Aa + (1 - p)^2aa$, in which p is the frequency of one of the genes (*A* in the example), 1 − p the frequency of its allele. The validity of this calculation rests on the assumption that fertilizations are made strictly at random.

   The steps above are outlined on the assumption that gene frequencies are known, but in practice that is not immediately true. One determines the frequencies of genes by counting individuals in the population and reversing the calculation. One must know how the character in question is inherited, whether there is dominance and which gene is dominant. Suppose that 16 per cent of a population shows the recessive character *a*, hence that they are of genotype *aa*. The frequency of gene *a* must therefore be $\sqrt{0.16}$, or 0.4. That would mean the frequency of *A* is 0.6. Then, by squaring the frequency binominal, the expected frequency of the several genotypes would be found to be 36 per cent *AA*, 48 per cent *Aa*, and 16 per cent *aa* (the last having been determined by the census).

   Genetic Drift. If both alternative genes *A* and *a* were abundant and well distributed through the population, there would be an "expectation" that in the next generation they would have the same frequency. But "expectations" are averages, and no average of many possibilities is ever likely to be exactly realized. The next generation is almost certain to have more than the expected fraction of one of the alternative genes, less than expected of the other. Either one may have gained. The shift may come from several sources. Not all individuals are likely to reproduce, and those which do may be more largely of one genotype than is expected. Those which do reproduce may not leave families of equal size, and the larger families may come from parents having a greater frequency of one of the genes. When the eggs of heterozygotes mature, one gene at meiosis may go more than half the time to the polar body. In fertilizations, one kind of sperm may enter with more than proportionate frequency. Not all fertilized eggs develop, and the losses may hit the two alleles unequally. Other accidents may help to change the proportions of *A* and *a* among the survivors.

The direction of change in frequencies may well be reversed the next generation. There is likely to be fluctuation in both directions over a period of generations. If these fluctuations of opposite sign balanced one another, there would be no *net* change, though all the fluctuations would be regarded as evolution. It would be *possible*, however, for the shift to go farther in the same direction for a number of successive generations. In the untold generations of millions of species of organisms, it would be surprising if there were not sometimes a succession of changes of the same sign. Small evolutionary changes may thus be purely accidental.

Reference was made in the preceding chapter to the decline in frequency of genes that are already in a small minority, particularly in small breeding populations. This sort of decline was excluded from the above example by stipulating that the two alleles were abundant and were both well spread through the population, so there would hardly be any portion of the range in which one gene was lost in one generation. This downward course of minority genes is part of the same general change referred to in this section—random change of frequency. Some evolutionists have applied the name "genetic drift" merely to the random loss of variability through complete elimination of genes that are already infrequent. The name "drift," however, is more fittingly applied to any kind of random change of frequency.

Mutation Pressure. The chief obstacle to the loss of variability through drift in frequencies is the tendency of mutations to occur again and again, already referred to as proof that mutation is directed. So many genes in Drosophila have mutated a number of times in the same way that one may well ask whether all genes are not thus mutable. Such a suspicion would be supported by the structure of the gene, discussed earlier. Some Drosophila mutations have occurred so often that geneticists have lost track of the number of times. After many repetitions, the recurrences were no longer reported. Other organisms furnish examples. One locus in the chromosomes of a particular strain of corn mutated in about 1 germ cell in 500, usually in the same way. Rats have produced a few repetitions, and the induced biochemical mutations of the mold Neurospora have sometimes been identical with earlier inductions.

Man experiences repeated mutations to hemophilia, chondrodystrophy, retinoblastoma, sickle-cell anemia, and other defects. Hemophilic men mostly die before maturity, so that a large fraction of the hemophilia genes are wiped out in each generation. Yet hemophilia seems to maintain its prevalence. To keep up its frequency, it would have to

arise by mutation in 1 X-chromosome germ cell in about 35,000 in each generation. The rate for chondrodystrophy is computed at about 1 in 25,000, for amaurotic idiocy 1 in 25,000, for aniridia 1 in 140,000, for epiloia 1 in 165,000, for retinoblastoma 1 in 70,000, for thalassemia 1 in 2500, and for sickle-cell anemia 1 in 1000 in American Negroes. This last-named disease is due to one gene lacking dominance, in that the homozygote has sickle-cell anemia (Fig. 101), a serious disease, while the heterozygote has no important pathological condition, though the red cells do sickle, less markedly.

The influence of repeated mutation of a given gene on evolution is called *mutation pressure.* If this pressure were unopposed by any other
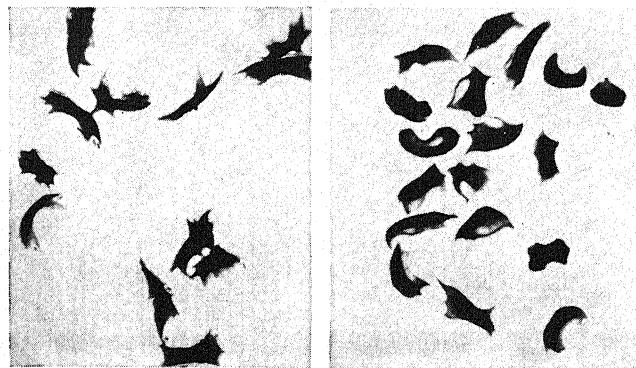
Fig. 101. Red blood cells in sickle-cell anemia (*left*) and sickle-cell trait (*right*). Former is homozygous, latter heterozygous, for same gene. Sickling occurs in drawn blood and sometimes, in the homozygote, in the circulation. (*Courtesy of Dr. James V. Neel.*)

factor, the gene produced by the mutation would eventually replace the one from which it comes. Usually, however, such mutation is opposed by reverse mutation. If B mutates to b repeatedly, it is usually true that b sometimes mutates back to B. Under these circumstances b would not replace B. The two mutation rates are ordinarily not equal, the reverse mutations being the less frequent. If the mutation of B to b occurs at twice as great a rate as the mutation of b back to B, gene b would increase in frequency until it was in two-thirds of the pertinent chromosomes. Then the population would be in equilibrium, since the mutations in opposite directions would be equally numerous.

The net effect of recurrent mutation is usually to prevent permanent loss of variability even in the small populations where such loss is most likely to occur. Seldom is it powerful enough to effect any permanent

change by itself. It is always opposed by something, and among the opposing factors may well be one which outweighs recurrent mutation many times over.

Other Mutational Guidance. Directing evolution by recurrent changes of a gene to some particular one of its mutant forms is limited to increasing the frequency of the mutant gene. There are suggestions that under some circumstances the effects of repeated mutation may be more varied. Genes that cause mutations were mentioned in the chapter on primary change. Sometimes these genes cause more mutations at certain loci than at others. A stock of Drosophila from Florida has a high mutation rate because of a certain gene in its second chromosome,
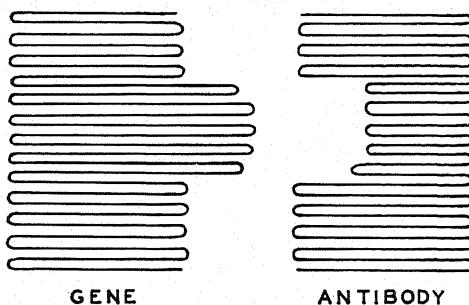
GENE   ANTIBODY

FIG. 102. Hypothetical folding of long protein molecule to form antibody having a configuration complementary to that of a gene.

but the effect of this gene is not spread evenly over all loci. Certain genes are "favored." The second-chromosome gene *could* exert quite an influence over long periods.

The effect of antibodies in causing mutations in Neurospora, mentioned in the account of artificial induction of mutations, suggests another internal control of evolution. The antibodies were produced in rabbit serum, against Neurospora extracts, and Neurospora was then exposed to these antibodies. Of the 25 modifications produced, and given the segregation tests to see whether they were mutations or some other sort of physiological change, 11 turned out to be mutations of the same gene. The explanation suggested is that antibodies were produced (Fig. 102) in relation to the configuration of this particular gene, and then because of their physical similarity the antibodies were able to modify the gene. The question arises whether, without antibodies artificially introduced, a gene might not occasionally create in the cell something nearly enough in its own image to react on the gene that produced it. The gene would in a way be guiding its own evolution.

Successive changes in the same direction have been reported for *Staphylococcus aureus*, the bacterium of certain abscesses. Mutations providing resistance to sulfonamide have occurred, and a succession of these mutations has furnished stepwise increases in the resistance. The rate of mutation was of the order of 1 per billion bacteria per generation. Some other modifications of bacteria could be interpreted as responses to the environment, but some of these might prove to be only selection of strains already in existence. Much interest attaches to the discoveries being made regarding the genetic mechanism of bacteria and the nature of their mutations. The interest centers in the question whether bacteria, unlike other organisms, experience environmentally produced modifications which fit them for the environment that produces the mutation—whether environment induces direct adaptation to itself. We return to the question of adaptiveness of mutation in bacteria in a later section.

The successive steps in one direction mentioned above might be regarded as a primary type of orthogenesis—evolution in a straight line, directed by an internal agency. One student of Drosophila thought he had discovered such mutational orthogenesis when, after heat-treatment, he obtained a succession of mutations causing darker and darker body color. Other investigators confirmed the production of mutations by heat, but did not observe successive changes in the same direction. It is not likely that any of the supposed instances of orthogenesis on a large scale, as conceived by some paleontologists— perhaps the evolution of the horse or of the dinosaurs—got their start from orthogenetic mutation.

Migration. The transfer of individuals from one population to another tends to increase variability, as explained in the preceding chapter. In a small way it *could* lead to change of gene frequencies. When individuals migrate, they are not likely to carry exactly the same proportion of the alleles at one locus as characterizes the population to which they belonged or the one to which they go. Their subtraction and addition thus change the gene composition of both populations. If the migrants are not joining a new population, but are entering an unoccupied area (as in expansion), their gene frequencies set the pattern for later generations—to follow or depart from as in any other population.

These changes may be random and migration be just another way in which the direction of evolution is determined by accident.

Adaptiveness of Living Things. Looking back over the factors of guidance so far listed, one sees nothing that relates the nature of species

in any definite way to their environment. The nature of mutations, being determined by molecular structure of the genes, does not depend on the character of the agent which induces the mutations. None of the X-ray mutations of experiments has any bearing on the life of the animal in an environment full of X rays. The rodents which mutate in the same way are not doing so because ruby eyes and yellow fur are of any concern in the world in which they live. Repeated mutation of the same gene in the same way is not a reaction to a type of environment, nor is the return of a mutant gene to its former state such a reaction. The drift of gene frequencies, being accidental, is of no help to a population in solving its problems of existence—it may even be against the population's interests. Migration of individuals into places better suited to them could explain some fitness, but the amount of adaptation obtainable in that way must be strictly limited.

In the bacteria, as already indicated, there are hints that perhaps environment is adjusting organisms to itself, though varying interpretations have been put upon what happens in them. One illustration must suffice. In Pneumococcus, virulent strains produce about themselves a polysaccharide capsule which protects them from attacks by phagocytes. Other strains lack the capacity to produce such a capsule (Fig. 103). Capsules of different strains are chemically dissimilar, as shown by the unlike antibodies they induce in serological tests. These differences are genetic, since each strain maintains its characteristics. Mutations occurring in encapsulated strains have occasionally reduced or destroyed the capacity to form a capsule, and the new condition is as permanent as are other strain characteristics. Now, one of these unencapsulated strains may be made to produce capsules again by injecting them into mice along with (or exposing them in laboratory cultures to) dead cells of a capsule-forming strain. Furthermore, the capsule which the cells may now form is of the chemical type of the injected dead cells, not necessarily of the type which the strain had previously produced. The injected capsules are not merely restoring to the strain its ability to produce capsules again but are determining what sort of capsules they shall be. The direct transforming agent is not the polysaccharide of the capsule but a desoxyribonucleic acid. This action has been interpreted by some as environmental guidance of mutation, bordering on the old Lamarckian idea of acquired characters. It is possible, however, to explain the results (as Taylor has done) as merely the transfer of some sort of genetic unit from one strain to another. Under this concept the change would not even be a mutation. It would be rather a transfer of genetic material comparable to that

which occurs in hybridization. The genetic mechanism of bacteria would have to be different from that of most other organisms, but there are other grounds for assuming that it is different.

The lack, in most organisms, of any contribution to adjustment to the environment is a weakening feature of the guiding agents so far mentioned, because animals and plants are so well adapted. Organisms
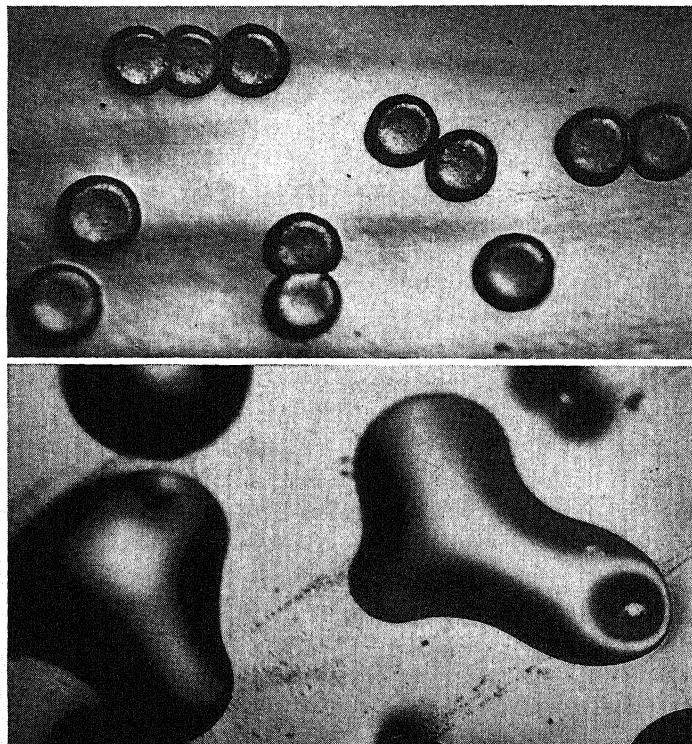
Fig. 103. Encapsulated (*below*) and unencapsulated strains of Pneumococcus, enlarged 20 diameters. (*Courtesy of Dr. Harriett Ephrussi-Taylor.*)

all live in approximately the right situation, including favorable temperature, the proper moisture, a continuing food supply, absence of too many enemies or presence of suitable means of protection from them, no greater fluctuation of these features than the plasticity of the organisms can endure, and perhaps social organization to supplement the contribution of the environment. A catalogue of the adaptations of living things would run the gamut of all natural history. To many biologists, fitness to the environment has seemed the central theme of

their science, because that fitness is so prevalent. The guidance of evolution has resulted in species well adapted—sometimes marvelously adapted—to their surroundings. Such fitness cannot be accidental; it must be produced by a powerful agent. That agent is held to be natural selection.

Natural Selection. The qualities of animals and plants are masters of their own fate but quite without design from any source. Individuals and populations are not alike; mutation, chromosome reorganization, recombination, and migration provide differences. Some of the differentiating properties are more persistent than others because they are part of the scheme that makes them persist. The older selectionists regarded "usefulness" as the touchstone of permanence and concluded that advantageous qualities would be preserved. Usefulness, however, is relative; it may be measured in relation to different things, not all of which concern evolution.

Evolution, as we have seen, consists largely of changes in gene frequencies. Anything that causes a given gene to become more frequent might be said to be "useful" to the gene that is thus increasing; that is the only usefulness there is in natural selection. Frequency of a gene can be increased only by increasing the proportion of individual organisms carrying that gene. If the gene confers on an individual the capacity to leave more descendants, which will likewise carry that gene, it will come to be in a larger proportion of the chromosomes containing its locus. If the advantage is a permanent one, the increase of individuals will continue over the generations. Such increase is probably never steady, in the sense that *every* generation includes more individuals with the gene in question than did the preceding generation. The selective advantage would have to be very strong indeed to guarantee progress in every generation. Evolution would be guided with almost explosive speed if the advantage of any mutation were great enough to ensure an increase of its representation in every generation. All that is required is a *net* increase over a series of generations. Most advantageous genes in nature probably do not possess to a high degree the capacity to increase their own numbers. Most advantageous genes could probably not be proved, statistically in an experiment, to have that advantage. This means simply that the advantage is usually small; more highly favored genes may now and then arise, but presumably they cannot be common.

Establishment of New Genes. When a gene mutates, its new form exists in only one individual, which is a heterozygote. If the mutation is of a recurring type, it is conceivable that it might appear more than

once in the same generation in a species consisting of millions of individuals; but two like mutations can hardly arise at the same time within one breeding population. Any mate of the heterozygous individual must therefore be a homozygous unmutated one. Half its offspring should likewise be heterozygous bearers of the new gene, and some of these may luckily be among the ones that survive to produce the next generation. These heterozygotes, because they are still rare, will again mate with homozygous "normal" individuals, and their heterozygous offspring again have a chance to be among the survivors.

If the new mutation is strictly recessive, as we generally judge it to be, all these possible survivals are entirely independent of the influence of selection. It makes no difference whether the gene is of a sort that would favor more descendants, or fewer descendants; if it is completely recessive, it cannot exert that favor or disfavor in a heterozygote. New mutations are mostly lost. There are so many more wild-type genes than mutant ones in each breeding population that the mutation has small chance of surviving. Still, it has a chance; and if the mutation recurs, its total chance is increased. If it recurs frequently enough, it has a very good chance of becoming a permanent part of the variability of the species.

If in addition to luck and recurrence the new gene favors the production of more descendants, it is practically sure, sometime, to succeed. It has to pass over the early stages of survival by luck alone. Frequent recurrence ensures that luck. When the gene becomes frequent enough for heterozygotes to meet and mate, homozygous mutant individuals appear. Then for the first time its selective advantage comes into play. That advantage may be measured by the increase in the proportion of the pertinent chromosomes containing the new gene. To say that a gene has a 1 per cent advantage means that the fraction of the chromosomes containing it is 1 per cent greater in any generation than in the preceding generation. It may be computed, as Simpson has done, that a gene which has a 1 per cent advantage, and recurs at the rate of one in a million each generation in a population of 10,000,000 is sure to become established in 25 generations. With the same advantage and same rate of mutation, but in a population of only 10,000, the gene might require 25,000 generations to become established.

Recessiveness in Question. While new mutations usually appear recessive, it is not certain that they are strictly so in their evolutionary bearings. We judge of recessiveness by what we see, and the vermilion eye and vestigial wing of Drosophila certainly do not appear to any degree in heterozygotes. The visible expressions, however, are not

the important features of these genes so far as evolution is concerned. Vermilion as an eye color probably neither helps nor hinders a fly; and there is no serious physiological handicap of such flies, for they are healthy and the vermilion gene is found in natural populations. Vestigial wing as an adult character is a disadvantage, since flies with such wings cannot fly. Yet the great disadvantage of vestigial is in its physiological effects. There are never as many vestigial-winged flies as would be expected in a genetic experiment involving that character. The flies homozygous for the vestigial gene are subject to high losses during development—before there are any wings. The gene for vestigial is known to influence such things as rate of oxidation in the wing rudiments, and it may have other, unsuspected, physiological effects. The damage done by these physiological activities is presumably much greater than that resulting from the inability to fly.

With respect to these physiological features it is not so certain that new mutations are wholly recessive. It would take very extensive tests of heterozygotes to prove that they were physiologically identical with the wild-type fly, and such tests have not usually been made. Heterozygotes may conceivably show some effect of the new gene. If this were true, selection would not have to wait so long to begin to operate for or against the newcomer. It would not need to await the production of homozygotes. Some evolutionists have accepted as likely this lack of complete recessiveness and have felt entitled to suppose that natural selection can start operating on a small scale at once after a mutation arises. How important this possible feature of mutant genes is depends on the degree to which they affect heterozygotes, and on this question there is little reliable information.

Why Mutations Are Recessive. The statement has been made several times that mutations are usually recessive. Partly it rests on observation; mutations studied have mostly proved to be recessive. This empirical basis of the statement is more substantial for Drosophila than the mere record of recessiveness indicates. In these flies less than 10 per cent of the genetic changes are dominant, and many such dominant changes are not mutations of genes; they are chromosome reorganizations instead.

The observation that most mutations are recessive has led to theories concerning the reason for that recessiveness. The arguments usually take the form of showing why the wild-type genes are dominant. They seek to show that selection is itself responsible. The wild-type characters are the advantageous ones; that is why they have been preserved to such an extent that we call them wild type. Anything that would

make these advantageous characters come to expression in a larger number of individuals would be favored by selection.

One form of the general theory of dominance is that complex systems of, say, enzyme interactions have been gradually set up. Complexity of the enzyme system leading to the expression of an advantageous character is a factor of safety—a sort of insurance that the character will be expressed. Assuming that mutations have furnished these enzymes, one would conclude that selection would have built them into the complex system that now exists. With such a complex system, mutation of only one of the two genes in an individual would be less likely to interfere than would mutation of both genes. That is, the system is so effective that defection of one gene's contribution does not change the expression of the character.

Another form of the theory that dominance is produced by selection rests on genes that modify dominance. Genes that modify dominance of other genes are known in cotton, Drosophila, mice, and poultry, and they are probably fairly common. Sometimes the only known effect of a gene is to make an otherwise recessive character show to some degree in a heterozygote. Suppose, now, that a new mutant gene turns out to be useful—in the sense of leaving more descendants—and that it is recessive. Should modifiers appear that would make the useful feature appear to some degree in heterozygotes, the modifier would tend to be preserved in more individuals. Other modifiers of dominance of the favorable genes, if they arose by mutation, would be accumulated by selection, until the once recessive character would now be dominant. Also, because it favors more descendants, it has replaced its alleles and is now the wild-type gene.

As for the mutations that occur sporadically now, they have been occurring all along. Had they been useful—producing more descendants —they would have become dominant. It is assumed that modifiers of dominance—so the theory goes—are at the beck and call of natural selection. According to this theory, genes are still "mutations" (that is, not wild-type genes) because they are not useful, and they are still recessive because they are not useful.

It is interesting that the evolutionists who most favor the dominance-modifier theory, which should lead to complete dominance of wild-type (useful) genes, are the ones whose views of the early action of natural selection require that wild-type genes be not quite dominant. These two requirements are not mutually exclusive if it be accepted that the dominance that is favored by usefulness is not quite perfect. Perhaps it could be assumed that a nice balance, possibly a shifting one, exists

between the need of making greatest use of beneficial genes and of leaving open the opportunity of getting still more advantageous ones.

Competition. While much of the fundamental operation of the principle of selection is included in the preceding sections, some consideration must be given to its results in natural situations. Charles Darwin and Alfred Russel Wallace (see Chap. I) conceived the theory without reference to mutation, reorganization of chromosomes, or recombination. They knew nothing of the genetic mechanism and so were handicapped by the then prevailing view that heredity was a blending process—that in a hybrid the qualities of the parents were irretrievably mixed. They knew that there was variation and assumed that some of it was inherited. Their theory of natural selection was built upon these concepts.

Both Darwin and Wallace were led to the natural-selection idea by reading Malthus, whose theme was the geometric increase of populations, leading to competition between individuals, or between populations, or between species. Competition has figured prominently in most evolution discussions since their day. The idea has probably been overworked; certainly the word has been used where it is not pertinent. The relation between two animals or other units is competition if both require the same thing, and the supply of that thing is limited, so that the more of it is consumed by one of the competitors the less there is left for the other.

Two strains of yeast mixed together in the same culture have been described as competitors. If limitation of their growth is effected by the alcohol which both of them produce, and that limitation is more severe for one of them, selection operates, but their relation seems hardly to be competition. When cactus invaded a new area that became dry because of 10-year vagaries of the weather, and then disappeared from it when rains returned, it is not clear that the cactus was in competition with its successor grasses for water and light. Perhaps the wetter conditions were simply not suitable for cactus. When a cuckoo, which is hatched in the nests and fed by the adults of other bird species, pushes the young of the host species out of the nest, that action is hardly any more competition than is predation. If the cuckoo appropriated more than its share of proffered food, and the host nestlings starved to death, their relation could be called competition.

The word competition can be very misleading in situations where it may not be actually wrong. One of the competitions which the high reproductive rates are said to create is competition for "room." It is true, if such reproduction were not in any way opposed, the earth or

the universe would not be big enough to hold all the products. But long before all available space was occupied, there would almost certainly be set up in the crowded individuals the modified physiological states that would prove the downfall of some of them. While these individuals were competing for "room," they would be dying because their genetic make-up could not cope with the imposed physiological conditions. "Room" as an object of competition does not represent the biological situation. Quite different is the rearing of two species of Paramecium together in a culture with controlled alkalinity and with fixed (and deficient) amounts of bacteria as the sole source of food. This seems to have produced real competition. In such tests *Paramecium aurelia* always won over *P. caudatum.*

Competition doubtless exists in nature, and there are ecological devices that seem to minimize it, these devices being presumably the result of selection. But selection *can* work without competition, and it seems likely that it often does. Suppose that, in a given situation, the number of individuals is kept down purely by accident, all genetic types being proportionately represented among the survivors of the accidents. Assume that food and other required things are in ample supply for all that survive. Any genetic combination resulting in greater reproductive potential would be favored by selection, but without any competition.

The mere existence of two unlike types together, one of them succeeding, the other failing, does not prove competition. The nature of the relation between coexistent forms needs to be reassessed, particularly where it has heretofore been judged to be competition.

Avoiding Enemies. From the beginning of selection theory, one of the favorite qualities which selectionists sought to explain was ability to elude enemies. The criterion of success through selection—leaving more descendants—is clearly involved in avoidance of predators, since one of the surest ways of leaving few descendants is to be eaten before many are produced. Naturally those devices which repel enemies, such as the spines of a porcupine or the hard sectional shell in which the armadillo rolls itself up, received attention. Disconcerting an enemy, as a squid may do by ejecting a cloud of ink in its face, was an appealing selective process. That animals are overlooked by predators through resemblance to the environment has been proved experimentally in a number of instances. Dice and others have shown that dark races of mice live in areas of black lava beds, lighter-colored races in sandy areas, and that owls capture fewer of those which resemble their background. Sumner took advantage of the capacity of certain fish

to change their color in response to their surroundings, darkened some of them and lightened others by keeping them in black and white tanks, respectively, then exposed mixed lots (Fig. 104) of dark and light fish to predatory birds. In dark tanks more of the light ones were captured, in white tanks more of the dark fish. Similar results were obtained by others with grasshoppers against similar or contrasting backgrounds,
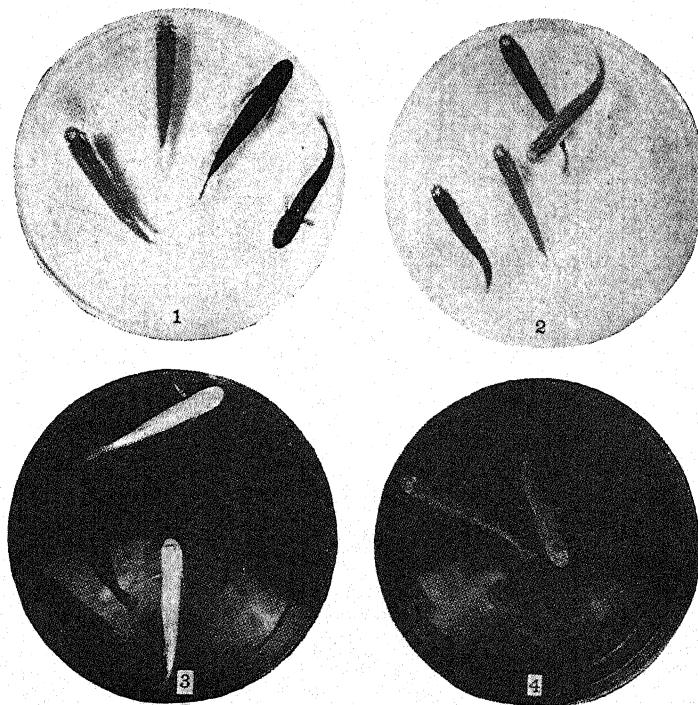
FIG. 104. Protective coloration, experimentally demonstrated. Light and dark fishes on light and dark backgrounds were unequally subject to capture by predators. (*From Sumner in American Naturalist.*)

with domestic and wild birds as the predators. It is inferred from such results that similarity to background has been developed through natural selection—that the ancestors were not of the present colors or shades. Dark forms of certain moths in England and Germany are found to be more vigorous than the lighter ones, but have become predominant only in the vicinity of large cities where the general landscape is darkened by industry. This is interpreted as a result of protective coloration.

Warning color, supposed to confer conspicuousness on animals which are already protected by some disagreeable or dangerous quality such as a sting or unpleasant taste, is thought by some to have developed under the influence of selection. The ancestors were supposedly not so colored, but as mutations to color came into being predators were supposed to have used the color as the mark of unpleasantness and to have spared many of the colored mutants—after learning by experience, of course, that a bad taste went with the color. The most thoroughly investigated instance of supposed warning color turned out not to be such. Brilliantly colored small coral-reef fishes are actually left severely alone by the gray snapper, a predatory fish—so long as the colored fishes stay near the reefs. Taken out into the open, these same colored fishes are eaten greedily. The snapper was proved to have color vision and a memory; yet the color is not a warning to it in open water. Reighard, who made the tests, concluded that the immunity of the small fishes near the reefs was dependent on the food-taking habit of the gray snapper. This fish takes its prey with a vigorous rush. It would not make that rush when there was a reef just beyond its intended victim.

Mimicry, the resemblance of a supposedly edible species to a not closely related warningly colored species, is held by many evolutionists to have arisen through selection. Experimental evidence relating to the edibility of the mimic, inedibility of the model, behavior of supposed predators, and the extent of genetic difference between the mimic and its nonmimicking near relatives is very meager.

Not all color resemblance is related to escape from enemies. The butterfly Oeneis in the Sierra Nevadas is of different colors related to the prevailing color of the rocks, but no predator that could account for this similarity is present. Nor is selection that affects color varieties necessarily based on the color. Red and black lady beetles, the former dominant, near Berlin fluctuated in number during the year, red being favored in winter, the black ones in summer. Nothing in the environment seemed to indicate that color was important; presumably some physiological difference associated with the color was the basis of selection. Color varieties sometimes differ in behavior. Hovanitz finds that the white variety of the butterfly Colias flies earlier in the day than does the orange type, from which the white differs by just one gene. No selective action has been discovered here, but if there were selection, the investigator might attribute it to color when really it stemmed from behavior. Speculative evolutionists are exposed to many such pitfalls.

The enemy-prey aspect of the food problem has its converse component, that of getting food as opposed to that of being food. Ability to obtain food is a universal requirement, but so much of it is unspecialized and unspectacular that it is not considered here.

Resistance. Ability to withstand the untoward conditions that environment imposes has been constantly under the influence of selection. With most of the results of this selection we cannot deal. Some instances of it, however, have been so recent, so patent, or so striking as to have special interest.

Scale insects, pests in orchards, have progressed in their struggle with man by developing strains more resistant to insecticides. The red
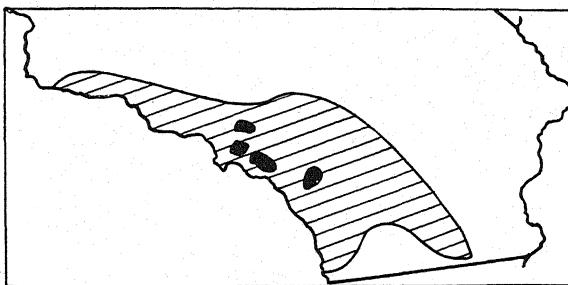
FIG. 105. Range in southern California (shaded) where red scale was almost eliminated by fumigation, only to be succeeded by more resistant strain preserved in the black areas.

scale, brought under control in California by fumigation with hydrocyanic gas, soon brought forth a strain resistant to such treatment. The resistant strain, differing from the susceptible one by just one gene, was already present but in such moderate numbers as not to be a pest until the susceptible type was removed (see map, Fig. 105). Each within a very few years, San Jose scale became resistant to lime-sulfur spray, codling moth to arsenical sprays, screwworm to phenothiazine, and citrus thrips to tartar-emetic-sucrose spray. Either resistant strains were long present or arose in time to produce the newly resistant types. Experiment stations have developed wheat varieties resistant to rust, only to find new strains of rust arising to which the wheat was no longer resistant.

Ecological separations are effected by differences in resistance. Crayfish of the kinds that live in ponds tolerate a low oxygen content of the water; the kinds that require more oxygen live in streams. *Drosophila pseudoobscura* lays more eggs in a lifetime at rather high temperatures,

D. persimilis more at low temperatures. The summer distribution of the two species is governed by that difference. Different strains of *D. funebris* are of unequal viability at different temperatures. Hibernation of this species helps eliminate the less fecund females, so that the survivors lay more eggs the next season. Strains of a parasitic wasp were separated by selection in the laboratory, one doing best at 9°, the other best at 25°C.; strains in nature were then found to differ in the same way, located in areas that differed thus in temperature. Frogs whose eggs develop best at low temperature are found in northern ranges, those whose eggs develop best at higher temperatures live farther south. Such distinctions must have arisen by mutation and natural selection.

Evolution has been guided partly by extreme changes in conditions. A strain or species, to persist long, must be able to withstand those extremes. During a period of 50 years, the region of Sanibel Island, Florida, experienced nine severe freezes. All the fish of tropical species were destroyed in some of these, while the temperate types were not seriously harmed. If any species were reduced to several individuals in such a period, and the area were repopulated by them, the course of evolution could be very dependent on the genes of those individuals. The new population would carry not only their temperature-resistant genes, but other genes which might have no ecological significance at all. What has been regarded as an example of the effect of periodic extreme conditions is the distribution of the blue and white phases of the arctic fox. This species is spread around the polar area. The blue phase, made blue by a single dominant gene, is in a small minority in the species as a whole, but is the sole occupant of some small areas. These foxes are decimated every few years, as peak population densities are followed by famine or epidemic disease. No ecological difference has been discovered in the two color phases, so it is assumed that the disastrous periods have occasionally left only blue individuals as survivors, giving rise, on repopulation, to exclusively blue groups.

Resistance to disease is merely resistance to the living part of the environment. Probably every species subject to parasites has different degrees of resistance among its individuals. Gowen reports two strains of mice a thousand times as resistant to typhoid as were two other strains, also two intermediate ones. The resistant strains had more blood cells, both red and white, than the susceptible strains, and the intermediate strains had an intermediate number of cells. The red cells appeared to be more important than the white. Men, even races of men, have differed in this respect. Native tribes have often been more

susceptible to syphilis and tuberculosis than were the whites who introduced these diseases among them. Civilized man is rapidly reducing the selection pressure favoring resistance to disease, by discovering medical means of control. Here is one of the fields in which man is most likely to control his own evolution.

Regressive Evolution. What happens to characters developed under the influence of natural selection when they cease to confer any advantage? Some of them have degenerated. Cave animals are often blind, their eyes being either reduced or wanting. This is true of certain fishes (Fig. 106), insects, crustacea, and salamanders. Since mutations damaging to eyes occasionally happen in laboratory animals, it is as-
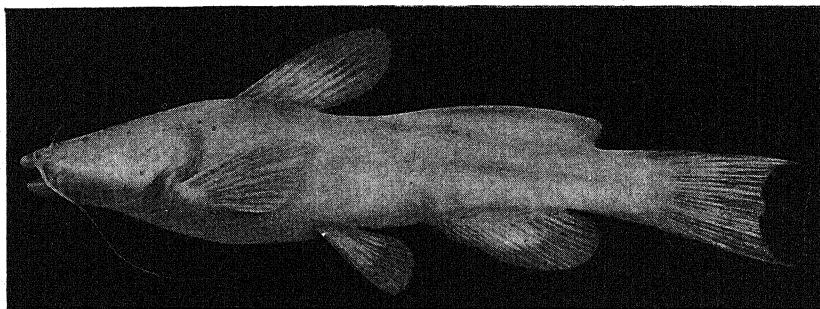
Fig. 106. Blind, unpigmented catfish, *Satan eurystomus*, from subterranean waters in Texas. (*Drawn by Grace Eager. From Hubbs and Bailey, Occasional Papers of Museum of Zoology, University of Michigan.*)

sumed that they happen in nature. Damage to eyes in caves would do little harm; hence there is no selection pressure against such mutations. In a Mexican cave, beginning near its mouth, there is a gradient of eyes in a species of fish, extending from normal eyes, through various grades of defect, to practically missing eyes farthest from the mouth.

Other vestigial organs are presumably to be explained in the same way. Selection does not work against mutations which damage a useless character. Parasites are largely degenerate for this reason. The barnacle Sacculina (Fig. 22), parasitic on crabs and deriving all its food from its host, has none of the crustacean characters in the adult stage. Only its free-swimming larva reveals its kinship to other barnacles.

Whether the action of selection is only negative, not supporting a useless character, or perhaps positive, as if getting rid of such a character would be an advantage, has been argued with respect to many

degenerate characters. The most common argument for positive action is that removing the needless organ would release energy of development for other purposes—an idea ridiculed by Walls as it relates to eyes, but perhaps supported by Lwoff for the synthesizing powers of bacteria. A mutation of Aerobacter conferred on that organism the ability to synthesize methionine but at the same time reduced its growth rate by 36 per cent. If methionine is always present in the environment anyway, such a mutation, though representing a sort of physiological gain, would be an evolutionary loss. The "wild-type" bacterium lacked the power to produce methionine but grew faster; perhaps that is why it became the wild type. Certain mutations in *Escherichia coli* have given this bacterium resistance to phages but at the same time deprived it of the power to synthesize *l*-proline. Whether *l*-proline is regularly present in the environment would determine the effect of natural selection on these mutations. Lwoff points out that, in general, parasitic microorganisms have lower synthesizing powers than do free-living ones. The hosts furnish the things the parasites need but cannot produce. The parasites may either have become parasites because they lost the synthesizing powers, or have become parasites and then lost the synthesizing powers because they could afford such loss mutations. Or, as in Aerobacter, they may have gained incidentally by loss of powers they no longer needed.
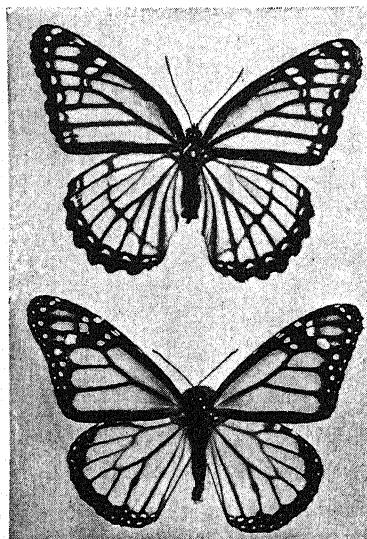
FIG. 107. Convergence of color (brown) and pattern in two distantly related butterflies. Viceroy (*above*) is held to mimic monarch (*below*). (*From Storer, General Zoology, McGraw-Hill Book Company, Inc.*)

Convergence. Evolution has sometimes been guided in such a way as to produce similarities, either of the whole body or of certain parts, between animals which are not closely related. The Tasmanian wolf, a marsupial, has general resemblance to the true wolves. The method of locomotion of kangaroos is not very different from that of various jumping rodents. A round tongue and reduced teeth are characteristic of ant-eating mammals, even though these belong to five different or-

ders—one each in the monotremes (egg-laying mammals) and marsupials (pouched mammals), and three among the true (placental) mammals. Tree-climbing birds of several different families have developed stiff tail feathers. Mimicry, the resemblance of two only distantly related forms (Fig. 107), may be included.

All but two of the illustrations of convergence here given involve things that actually are used. How important they are in the lives of the animals may be doubted in the other examples. Doubtless the useful ones have been the product of natural selection. An understanding of their evolution would require a knowledge of the genetic differences between at least one of the convergent forms and its near relatives, and such knowledge cannot be gained because crossing is impossible. Goldschmidt suggests that mimicking insects differ from their relatives by one gene, but others have disagreed.

In any case, the marvels of convergence relate not so much to the action of natural selection as to the production of mutations out of which such similarities can be built. Homology of genes, except perhaps between mimic and model, can hardly be counted on as a factor.

Rate of Evolution. Some features of rate of evolution are related to the guidance of the process. Rate of change of species must be commensurate with rate of change of the environment. Geneticists—particularly Drosophila geneticists—have sometimes pointed out the need of keeping mutation down. Too high a rate of mutation would

Fig. 108. Ring of chromosomes, and one pair, in a species of Oenothera which is perpetually heterozygous for the chromosomes in the ring. (*After Cleland.*)

be wasteful. Too much recombination would be similarly wasteful, since the unfit combinations would be lost. Chromosomes restrict recombination in inverse proportion to their amount of crossing over. When inversions are present, crossing over is checked in individuals heterozygous for them.

Most of what is known of inversion heterozygotes comes from Drosophila studies, and, for some of the combinations, being heterozygous is an advantage to these flies. Dobzhansky reports, for example, that flies homozygous for the standard chromosome arrangement of *D.*

pseudoobscura and *D. persimilis* (Figs. 86 and 87) are only about 80 per cent as successful as is the type heterozygous for standard and Chiricahua. Homozygous Chiricahua is less than half as successful as
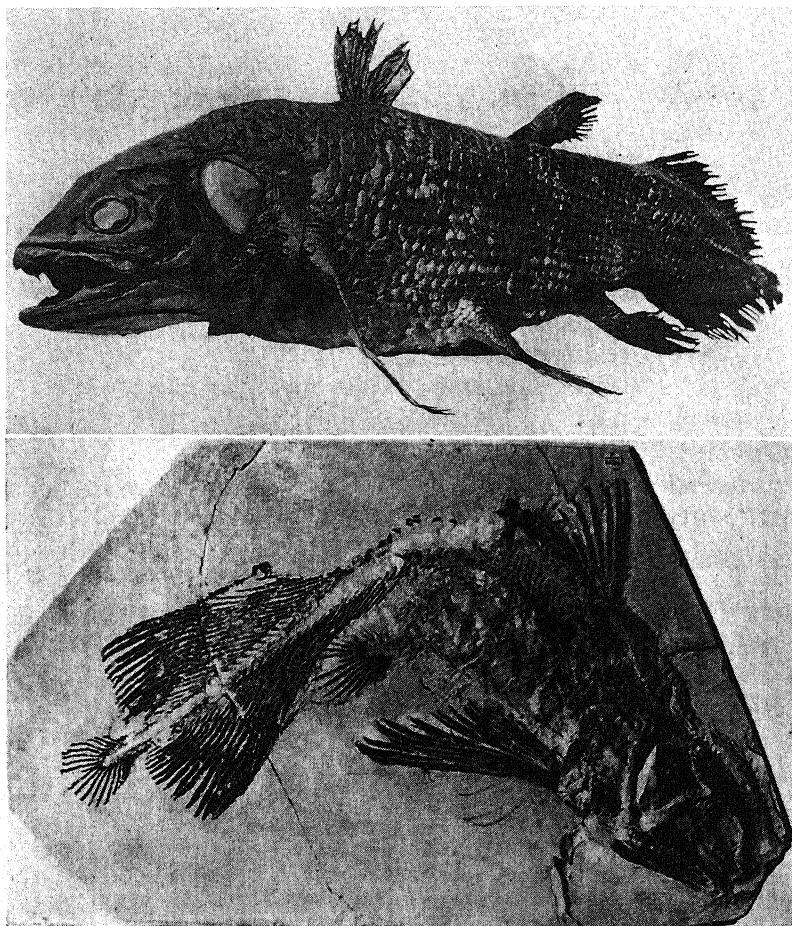
Fig. 109. The lobe-finned fish Latimeria, 5 feet in length, of a type long believed to be extinct since Cretaceous. *Below*, its fossil counterpart, the coelacanth *Undina penicillata* from Upper Jurassic of Bavaria. (*Above, from specimen taken by Professor J. L. B. Smith; below, from specimen in British Museum. Published in Illustrated London News.*)

the same standard-Chiricahua heterozygote. These distinctions prevailed at moderate but not at low temperatures. A number of other inversion heterozygotes that surpass their homozygotes in adaptiveness

are on record. Dobzhansky points to the suppression of crossing over by inversion heterozygotes as a means of helping to hold, unchanged, favorable combinations.

In many kinds of Oenothera (evening primrose) a comparable situation exists, as pointed out by Cleland. Reciprocal translocation has resulted in rings of chromosomes in heterozygotes (Figs. 108 and 89), and plants are kept perpetually heterozygous by death of one haploid chromosome group in the embryo sac, the other group in the pollen. Such heterozygous condition is beneficial, and Oenothera has profited by its very special mechanism.

In both Drosophila and Oenothera crossing over is prevented in the heterozygotes, and to this, it is suggested, is due the advantage observed. It should be pointed out, however, that Drosophila heterozygous for mere genes, not inversions, has been shown sometimes to have an advantage. Many hybrids have been proved to be more vigorous than their parent types. It can hardly be taken as proved that

Fig. 110. Horseshoe crab, Limulus, differing little from Triassic types. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc.*)

restriction of crossing over is the reason for the favor shown by selection to some of the inversion heterozygotes.

Very slow evolution is responsible for a number of primitive types still living. The lobe-finned fish Latimeria (Fig. 109) is of a type considered extinct since Cretaceous time, until it was found alive off the coast of Africa in 1938. A generalized lizard of New Zealand and a primitive termite of Australia are also little changed from old fossil types. Such forms are known as relicts. Little short of this condition are the horseshoe crabs (Fig. 110), about like some Triassic types; the brachiopod Lingula, almost changeless since Ordovician; the lungfishes (Fig. 28), much like those of Triassic; and the opossums (Fig. 27), only slightly changed from the Cretaceous. If we knew only these modern animals, and nothing of their fossil antecedents, we would be puzzled to guess what had guided evolution to such odd end products. Knowing the fossils, we can see that there has been almost no evolution to guide.

Views have differed as to where on the earth evolution tends to be most rapid. The Matthews theory of the origin of the mammals (see Chap. IV) was based partly on the assumption that a large northern

land mass would be a more likely place of origin because of the variable climatic conditions to which such a region is subject. Now, however, a number of evolutionists and ecologists hold that tropical regions are the scene of much more rapid evolution. The argument has nothing to do with the possibility that heat might produce more mutations. It rests on the thesis that many more ecological niches exist in the tropics. There are more situations in relation to which natural selection could mold races or species. There is plainly more variation in the tropics; but there are also more organisms to exhibit the variation. The tropics view could, of course, be correct for evolution in general without invalidating the theory of the origin of the mammals.

Nonadaptive Evolution. Enough factors of change independent of the environment exist to provide a modest amount of evolution that is not adaptive. Mutation pressure is one source of such evolution, since with the exception perhaps of bacteria and molds the nature of these changes bears no relation to the characteristics of the surroundings. Genetic drift, especially in small populations, could even go against moderate pressure of selection. Migration, accidentally affecting the frequency of genes possessed by the migrants, could be a source of nonadaptive change.

Characters that appear to be of no particular use are readily observable in many organisms. The A and B blood-cell antigens of man have no known value. The white and blue pelages of the arctic fox, already mentioned, are regarded as immaterial distinctions. Black leopards, much more common in Asia than in Africa, seem to be neither discriminated against nor favored. It seems likely that races or even species may often be distinguished by characters which give no advantage to their possessors.

Some evolutionists reject such a conclusion on the ground that perhaps the group distinctions have a use that we cannot detect. That is probably true sometimes. It is likely also true that some of the differences we judge useful really are not so. Sound logic should recognize both possibilities. The safest procedure is to assess the value of distinctions with all care and to adopt the conclusion to which they point. That procedure leads to recognition of some group distinctions as of no importance.

In the history of the evolution idea some biologists have felt impelled to assume orthogenesis—successive changes in the same direction guided by an agent within the organisms. Supposed examples of it have often had other possible explanations. Selection by a changing (or even a constant) environment could lead to straight-line evolution, but no

internal agent would be the guide. The evolution of the horse (Chap. V) is held by some to be an example of such "orthoselection." The difficulty of imagining any mechanism that would operate over long periods of time has worked against acceptance of orthogenesis. Repeated mutation could hardly carry evolution as far as the proposed orthogenetic changes. Haldane has shown mathematically how a quantitative character dependent on many genes could, if acted on by selection, swing past the stage which would be most advantageous before
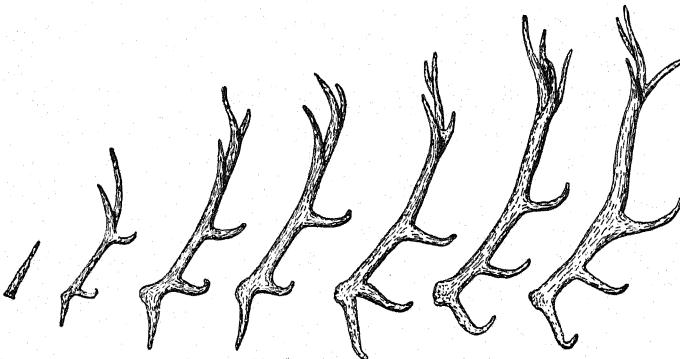
FIG. 111. Successive antlers of the wapiti, or American elk.

counterselection could check it. After such a check the evolution would be reversed and again go too far. The change would act like a pendulum, not go in a single direction.

What looks like orthogenesis is sometimes the result of selection of some character on which the attention is not fixed. The antlers of deer are an example. Large deer have larger antlers, with more points on them, than do small deer. The fact that antlers are shed annually enables one to observe that the same relation holds in the lifetime of individuals—older individuals have the more complicated antlers (Fig. 111). More complicated antlers go with large size. Now, many kinds of animals have grown in size as they evolved, so many as to lead to the conclusion that large size is advantageous. Size increased because of selection and carried antlers with it. "Orthogenesis" of antlers is but an incident to the orthoselection of bigness.

Mutations or recombinations must sometimes occur which, while not useful where they arose, would be useful in another environment. A change of that kind is called preadaptation, especially if the changed individuals happen to find the newly suitable situation. A wild potato in Mexico possessed genes for resistance to the wart disease and to the

blight fungus, neither of which enemies existed in its native area. The existence of these genes was discovered when the plants were taken to England. The resistance to both diseases has been introduced into cultivated varieties of potatoes. Students of blind cave fishes hold that the ancestors of most (but not all) such species were already to some degree adapted to life in darkness before they entered the caves. The emperor penguin, which lives below the Antarctic Circle, does not build nests—for one reason, because there is no nest material on the ice. It incubates its eggs by holding them up off the ice with its feet. This bird could hardly have ventured into such icy areas without first having evolved the foot method of insulating its eggs—probably in a region where nest materials were merely scarce, not lacking.

The nonadaptive origin of plant species by polyploidy must also be recognized. The steps which lead to doubling of the chromosomes can have no relation to the nature of the environment—certainly not in such a way that chromosomes would not be duplicated unless the new product were going to be an improvement. The new species suddenly formed must, of course, be able to survive. Natural selection could eliminate it. Yet even elimination would not be expected unless the polyploid form were less fit than the diploid form had been. The adaptiveness of the polyploid could even be slightly less than that of the diploid and not be at once rejected for that reason. Stebbins has called attention to the reduced significance of selection in the guidance of evolution of the flowering plants, because of the extent to which polyploidy has been the source of the origin of species in that group.

Effects of Atomic-bomb Radiation on Man. Because of the known production of lethal or injurious mutations by radiation of various types, concern has been expressed as to the effect of the explosion of atomic bombs—or even the industrial use and possible leakage of nuclear energy—on the direction of human evolution. It is assumed that man is as subject to radiation-induced mutations as are other animals and that by and large such mutations will be detrimental. It will be some time before direct evidence on these points can be obtained from human populations that have been exposed to atomic bombs; possibly no actual proof of such effects can ever be obtained in that way. Accepting, however, the likelihood that harmful mutations are so produced, some publicists have expressed the fear that as an extreme consequence the human race might be destroyed. Short of this dire result, they foresee the occurrence of many monsters—unless men mend their ways before it is too late.

The problem may be approached either from the population stand-

point or from the point of view of individuals. In either case many assumptions must be made before estimates are possible. One has to conjecture the rate of induced mutation, how injurious the mutations will be, whether they are recessive or dominant, or if not strictly recessive how much of their effect will show in heterozygotes, whether the mutations would affect reproductive rate or only the efficiency of the genetic make-up, and other things. The word "conjecture" correctly indicates what has to be done in studying the problem, even though something is known about the points named in Drosophila and other organisms. It would be easy to make assumptions which would lead to effects a hundred times as great as other justifiable assumptions would entail. Wright has made some of these assumptions and concludes first of all that, because of our lack of knowledge on so many matters, no judgment concerning the genetic and evolutionary effects of radiation on man can be taken very seriously. From the statistical or population standpoint, he can see no threat to the persistence of the human race deriving from any mutational effect of radiation. As it affects individuals who are exposed, and their descendants, he finds a strong possibility that cumulative doses of as much as 300 r could have important consequences and that even 30 r might not be negligible. Muller, who first demonstrated frequent X-ray mutation in Drosophila and who looks at the present problem of radiation effects from the individual and family viewpoint, takes a dimmer view of the outlook. He doubtless accepts Wright's estimates of probabilities, but even a given probability looks more serious to families than it does to the race as a whole. All investigators of the problem agree that it would be more comfortable if the effects of radiation on genes did not have to be faced.

ISOLATION

> The population . . . becomes the basic unit of taxonomy and
> the entire gene reservoir of an interbreeding local population
> forms the material basis of evolution. . . . Species can . . .
> be defined as groups of actually or potentially interbreeding
> natural populations that are reproductively isolated from other
> such groups.
>
> —ERNST MAYR, 1948

Though abundant diversity and striking fitness to the environment
are explained by the operations of the genetic mechanism, screened
by selection, there is one universal feature of living things that cannot
be accounted for by the phenomena so far described. That feature is
the separation of the rather distinct groups of organisms known as spe-
cies. The gaps which separate these groups, both as to their visible or
psysiological characteristics and as to their genes, require as explana-
tions either new phenomena or specialized extension of some of those
already considered.

What Is a Species? The problem now before us is involved—almost
stated—in the definition of species. Though taxonomists have long
argued the nature of species and still differ in the meanings they attach
to the word, elimination of some of the finer points at issue will give
us a workable concept. A species is a group of individuals which have
potential access to the same stock of genes. These genes have at least
an opportunity of flowing freely through any line of descent within the
species. Genes to which the members of a species do not have access
belong to another species. Some sort of separation exists between the
members of different species, such that the lines of gene descent do not
intermingle. This means, of course, that they do not cross.

To bring about commerce between such groups of genes, individuals
of different species would have to meet; in the higher animals they
would have to copulate; eggs and sperm would have to commingle,

then unite in fertilization; embryonic development would need to proceed normally, producing a functioning adult, which in turn would have to meet another individual, initiating a like chain of events. As between species, either the initial event does not occur, or some link in the chain is not forged. The stoppage occurs at different places for different pairs of species, but the effect is the same—the groups of genes are kept apart.

The general phenomenon of prevention of gene interflow is known as *isolation*. Some of the sources of isolation are imposed from without the organisms; some are within them. Examples of the more important ones will be reviewed.

Separation by Space. Individuals belonging to different populations do not mate if they never meet. Sometimes mere distance would preclude intermating even if there were no other obstacle. Usually there are ecological factors which keep the species more or less apart even though they are near one another. The cormorant and the shag, two bird species belonging to the same genus, are close together on the coast of Europe, but the former feeds in shallow water, on fish that live near the bottom, while the latter feeds in deeper water, on free-swimming fish. Two subspecies of the mouse Peromyscus are kept apart because one lives on lake beaches, the other in woods. Two species of mosquito (genus Anopheles) in Africa are separated by salinity of the water. The larvae of both can live in fresh water, but one of them can endure brackish water and, perhaps to avoid competition, usually does live in such water.

Sometimes topographic barriers keep species apart. The Grand Canyon separates two species of ground squirrel, also one species of pocket mouse from three other species. Certain fox and chipmunk species are partially separated by the canyon, but meet either above or below it. Some of the steamer ducks (genus Tachyeres) are separated by water. These ducks propel themselves rapidly over the surface of the water by means of their wings, used as paddles. One species is limited to the region around the Straits of Magellan at the tip of South America; another species is limited to the Falkland Islands. These two species do not meet. A third species, with better locomotion, occupies both of these areas and crosses the water between. It has maintained itself a single species. The falls of the Nile River effectively separate the stream fishes, and certain genera found in the lower course of the river are not represented at all above the falls.

Isolation by Time. Two species of cockleburs (Xanthium, Fig. 112) produce their flowers at different times. In one of them the flowers do

not open until after the seed capsules of the other are fully formed. Without any overlapping, they could not cross. Two species of Salvia are similarly separated by different times of flowering; but two other species of Salvia have overlapping flowering periods, and some hybrids are produced when the two kinds live together.

Specialized food habits separate two species of bees (genus An-
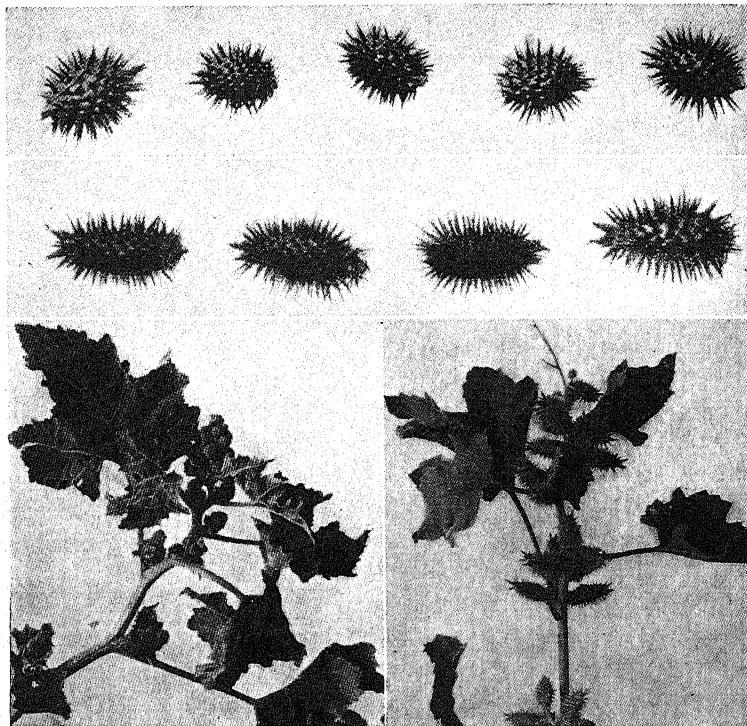
FIG. 112. Species isolated by different times of maturity of their germ cells. *Top row and lower left, Xanthium globosum,* whose flowers open after seed capsules are fully formed in X. *pennsylvanicum, second row and lower right. (From C. A. Shull in Botanical Gazette.)*

drena) in Wisconsin. They visit different flowers and are active at different seasons corresponding with the times of blooming of these plants. Two moth species feed on different plants which are in best condition at different times, but the moths emerge at different times in the spring so that food is not, at least directly, the separating factor. In two grasshopper species the isolation is definitely produced by the time of emergence. One of these species lives over winter in an imma-

ture form and becomes adult early in the spring. The other develops from eggs laid in the spring and matures much later. Even with this difference, there is an overlap of about two weeks in the periods when adults are found.

Two forms of sockeye salmon in British Columbia ripen the germ cells at different times. One form spawns in August and September, the other from October to December, both in the same lake. The late-spawning kind has a degree of immunity to a parasitic copepod not possessed by the other, and there is some difference in color. Such differences must arise because of lack of crossing between them. Taxonomically the two types are doubtfully considered subspecies of the same species.

Diurnal cycles of activity almost separate two species of fish in the rivers of Indiana and adjoining states. The white crappie is active in the daytime, the black crappie at night. They have similar habits and food and live in the same streams. Here the isolation is not complete, for interspecific hybrids are occasionally found.

Bars to Mating. Members of different species which live together and are mature at the same time are kept from mating by various factors. There has long been, particularly among entomologists, a belief that the copulatory apparatus is so constructed that that of a male would not fit a female of another species. This belief was named the "lock-and-key" hypothesis. It does not seem very well founded,

FIG. 113. Male genitalia of two species of lady beetle, *Hippodamia quinquesignata* (*left*) and *H. convergens*. These species have crossed and produced fertile offspring.

however. Two species of lady beetles (Hippodamia) in which the male genitalia (Fig. 113) are strikingly different have been crossed, and the genitalia themselves shown to be just one of the inherited characters. Three pairs of cumulative genes would account for the specific differences in these structures.

Some species are kept from mating by psychological (Mayr prefers the word ethological) differences. These are of different sorts. The courtship behavior of animals is designed, not to influence choice of mates, but to arouse readiness for mating. The courtship of animals of different species is usually broken off in early stages because the be-

havior patterns do not complement one another. A number of pairs of species of Drosophila have been tested, and there are few interspecific matings when members of the same species are available. The call notes of frogs and toads are found to keep species apart at breeding time. Patterns of display among fiddler crabs involve waving the chelipeds, raising the body, dancing, and other movements, and the details and combinations are different in different species.

The breaking off of courtship between species has sometimes been attributed to "species recognition," as if animals wanted their offspring to remain true to type. It seems more likely that the courtship simply did not arouse the desired reactions and was discontinued because it was ineffective.

Ethological barriers are often assumed when no others can be detected. Two species of mice (Peromyscus) breed freely together in the laboratory, and their offspring are viable. Yet in nature, though they meet over considerable areas, practically no hybrids are found. Two species of meadow larks are similarly interfertile indoors, but even with broad overlap of their ranges and habitats there is seldom any natural crossing. The mallard and pintail ducks produce fertile hybrids in captivity, but do not cross in their very wide area of overlapping ranges.

Conjugation in *Paramecium aurelia* is barred or ineffective as between certain strains. This species—regarded as a single species by taxonomists—is broken up into eight physiological species (usually so called though besides their isolation they differ in size, rate of fission, frequency of autogamy, and time and temperature of conjugation). Each of these species comprises two mating types. Two individuals of the same mating type never conjugate, but an individual of any mating type may conjugate with a member of the other mating type of the same physiological species. This phenomenon of mating types is not isolation; rather it is like sex in other organisms. Between the physiological species, however, there is isolation. Neither mating type of species 2 will conjugate with either mating type of species 6. The isolation of these two is complete, and the point of isolation is the prevention of mating.

An interesting point concerning the isolation of physiological species of *Paramecium aurelia* is that it may rest on a single-gene difference. There has been much discussion of the simplicity or complexity of the genetic isolation of species among higher organisms, with most evolutionists taking the position that it must (or does) rest on a number of genes. In *P. aurelia*, however, a single mutation may give rise to an isolated group.

Prevention of Cross-fertilization. Even when mating occurs there frequently are obstacles to union of the gametes. The obstacles are usually of a physiological nature. In many species of Drosophila the mucous membrane of the vagina swells markedly after mating. The swelling is stimulated by the spermatic fluid, even without any sperm in it. If the mating has been with a male of the same species, the vagina returns to normal size within a few hours. In an interspecific mating, however, it may remain swollen for days. A female which reacts thus strongly may not mate again. Eggs are sometimes destroyed in a swollen vagina, and in any case their fertilization is hindered. Certain pairs of species have this insemination reaction, as it is called, sufficently reduced to permit the production of some interspecific hybrids.

The amount of sperm introduced by a male of a different species may be less than in an intraspecific mating. This is true in *Drosophila pseudoobscura* and *D. persimilis,* as determined by examination of the spermatheca of the female after mating. Foreign sperm are also less viable in the passages of the female. These two phenomena should help reduce the number of interspecific fertilizations.

Often the reason for lack of fertilization is not known. The lady beetle *Hippodamia tredecimpunctata* copulates with another species of the same genus, but no hybrid offspring and no development of the eggs have ever been obtained from either of the reciprocal matings. Whether spermatozoa enter the eggs is uncertain.

In plants it is very common for the pollen tube to grow more slowly through the style of a flower of another species. If it arrives at the egg after the flower withers, there is no fertilization. Also, the style of another species may be longer than the one the pollen has to traverse in its own species. A cross between a short-styled species used as a female and a long-styled species as male succeeds better in Datura than does the reciprocal cross. Sometimes the tube bursts in a foreign style, and the sperm nuclei travel no farther. Sometimes pollen does not grow at all in a foreign style.

In certain marine animals, bringing germ cells together does not depend on behavior, growth, or reactions; the eggs and sperm are simply poured out into the sea water at the same time. While there may be some ecological separation of closely related species, this cannot be depended on to keep eggs and sperm apart when water is free to move. Eggs of sea urchins have been experimentally exposed to their "own" and foreign sperm and have experienced cross-fertilization less than 2 per cent as often as intraspecific fertilization. There is some block to fertilization by foreign sperm, some incompatibility between the cells

of different species. This hindrance may be lessened by changing the alkalinity of the sea water, but that scarcely explains the physiological nature of the protoplasmic barrier.

Inviability of Species Hybrids. If gametes of different species have succeeded in uniting, there still may be complete isolation of the contributing species. Some of the physiological species of *Paramecium aurelia* referred to in an earlier section are isolated in this way. Species 4 and 8 mate almost half as readily as do the two mating types of either of them, but none of the F_1 (exconjugants) survive. Species 1 and 5 mate about 40 per cent as readily as do different mating types of one species, and the F_1 are viable; the F_2, however, are almost completely inviable.

Fertilized eggs from attempted species crosses of fish have shown abnormal cleavage, elimination of chromosomes into the cytoplasm, and early death. The lady beetles *Coccinella novemnotata* and *C. transversoguttata* have rarely been crossed, and the fertilized eggs produced rather normal-looking embryos in the shell; but the hybrid larvae never hatched.

In certain species crosses of the Jimson weed Datura the pollen tubes reach the embryo sac, and the egg is fertilized, but no seeds develop. In one Datura cross the fertilized egg cleaves three times, to produce eight cells, then stops. The endosperm may develop farther than the embryo, and to such disharmony is attributed the failure of certain species crosses in wheat. In some crosses of flax species (genus Linum) a weak hybrid may be helped to grow by removing the seed coats. The growing embryo appears unable to break through these without aid. In other flax crosses removing the seed coats is not enough; the embryo has to be dissected out and put into a nutrient sugar solution. With that assistance it may develop into a self-maintaining plant in soil.

In crosses of certain moth species, only male hybrids survive. The females die in the pupal stage. In many species crosses there is a disparity of the sexes produced. Irregularities of the chromosome mechanism of sex determination is doubtless involved in all these instances.

Hybrid Sterility. One of the best-known methods of preventing the mixing of species waits to the very end of the hybridizing process before it interposes its veto. Hybrids may be formed, be vigorous, and have every appearance of being normal organisms, yet be sterile. Even if they are only partially sterile, they are at so great a disadvantage as compared with members of either contributing species that the transitional group is never effective. Interflow of genes between species is stopped or restricted to negligible proportions by this reduced fertil-

ity. One of the earliest-known species hybrids, the mule, offspring of
a female horse and a male ass, is a very vigorous organism, superior in
many respects to both of the parent types. Yet seldom are the repro-
ductive organs sufficiently normal to act as such. Fertility has no nec-
essary connection with general vigor.

The best-understood cause of sterility of hybrids is the irregularity
of the germ cells they produce. A clear case of intersterility due to
chromosome irregularity and nothing else is that existing between re-
lated plant species differing in their ploidy. Polyploidy as a source of
primary variation was described in Chap. VIII and some of its diffi-
culties pointed out. If a tetraploid species has arisen and achieved a
fair degree of stability through mutations that give it a functional di-
ploidy but with the tetraploid number of chromosomes, the tetraploid
species is at once more or less isolated from its parent diploid species.
Any hybrid of theirs would have three chromosomes of each kind, and
distribution of chromosomes at meiosis would necessarily be irregular.
The troubles arising from such irregular distribution were pointed out
in the earlier discussion of polyploidy; those troubles pertain equally
to hybrids of species with unequal ploidy.

Hybrids of species with the same number of chromosomes may be
partially sterile if the parental chromosomes are not strictly homolo-
gous, that is, if their genes are different or are arranged differently. The
chromosomes of such a hybrid do not pair, or pair only loosely. Without
such pairing, they are not distributed regularly in meiosis. Few of the
germ cells receive a single chromosome of every kind as they do within
species. Germ cells are of many different kinds, and fertilized eggs are
mostly not viable. The few normal cells they produce could, if lucky,
produce surviving individuals; but they provide only a very narrow
bridge for the transfer of genes between species.

Hybrid sterility resulting merely from lack of homology of the chro-
mosomes from the parent species is practically limited to plants. While
irregular distribution of chromosomes at meiosis may occur in hybrids
of animal species, something else, more fundamental, is almost always
involved. And in plant hybrids these more fundamental things are quite
commonly involved as well.

Sometimes there are genes producing intersterility, and these genes
act in a variety of ways. Sterility genes acting *within* a species are well
known, such as the "asynaptic" gene in corn. This gene prevents chro-
mosomes from pairing properly, even though these chromosomes are
strictly homologous. The result is irregularity of chromosome combina-
tions in the germ cells, and few viable offspring are produced. Many

plant species have recessive genes which impose sterility on individuals homozygous for them. Now, such genes could be imagined to create intersterility of species if the recessive sterility genes became dominant in the presence of a foreign genotype, that is, in a hybrid. Sterility gene *a*, harmless in its own species so long as it existed only in *Aa* individuals, would on crossing be in *Aa* individuals but then be supposedly dominant. Such species hybrids would, on the hypothesis, be sterile. Yet to produce any considerable proportion of sterile species hybrids, gene *a* would have to be fairly common in its own species. Being common, it would occur in many *aa* individuals, rendering them sterile. That would produce so great a handicap to its own species that natural selection would work strongly against the system. No example of this scheme is known.

A somewhat different one-gene isolating scheme has been proposed by Castle. It involves sensitization of a gene by its allele, a sort of anaphylaxis. Castle assumes that a new dominant gene arises in the inert part of a chromosome. This creates an allele in the opposite chromosome, likewise in the inert part, by sensitization. Having arisen by this method, these alleles will kill an individual which subsequently receives both of them. To act as a barrier to species crosses, each of these alleles would have to become incorporated in a separate population. How they would do this, when both arose in the same individual, is difficult to imagine; yet Castle points to crosses in chicory and peas which seem to him to support his view. To most geneticists the origin of a new gene out of inert material will probably seem more difficult than the separation, into different populations, of genes that are produced in the same place.

A more workable scheme is two sets of dominant interacting genes. Each set, by itself in one species, is harmless; but when the two sets are brought together in a species hybrid, the dominant genes interact to damage the reproductive function. Theoretically one dominant gene in each of two species would suffice to make such a scheme work. Actually, in the best-understood sterile hybrids, there are more of these genes. *Drosophila pseudoobscura* and *D. persimilis* when crossed produce completely sterile male hybrids and partially sterile females. While these species differ in four chromosome inversions, that is not the reason for the sterility of their hybrids. The trouble with the hybrids is not merely that their chromosomes enter irregularly into the germ cells; their whole maturation process is badly deranged. In one of the two reciprocal crosses, the testes of the males are small, indicating disorganization before the stage of chromosome pairing is

reached. Genes must be responsible for this situation. Appropriate genetic tests show that the disturbing genes are in most of the chromosomes; hence there must be a number of them. In backcrosses of the hybrid females to the parent species, sometimes there is only one maturation division, and spermatozoa are not produced. There is thus little chance for genes to flow from species to species even through the limited fertility of hybrids of one sex. Other Drosophila species produce similarly sterile hybrids whose gonads show degeneration prior to the time of pairing of chromosomes. This is true of *D. melanogaster* crossed with *D. simulans;* and when *D. pseudoobscura* is crossed with *D. miranda,* the male offspring have small testes and the females lay many
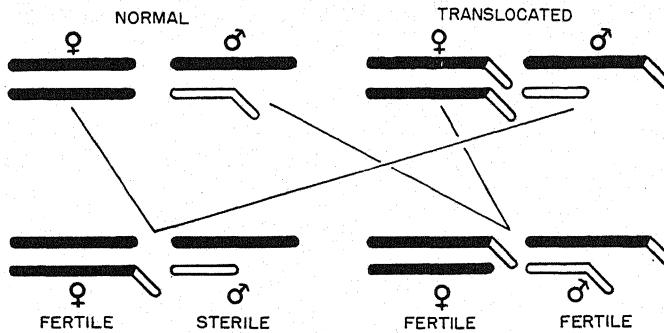
FIG. 114. Sterility of males produced by a racial cross involving a translocated segment of the Y chromosome in Drosophila.

eggs which seldom hatch. This evidence that sterility comes from genes, rather than from unmatched chromosomes, seems to be fairly general. Indeed, as stated earlier, hybrid sterility arising solely from chromosomal features is practically limited to plants.

Stern has used the fertility function of the Y chromosome in Drosophila to explain hybrid sterility of one sex in certain crosses where the other sex is fertile. From irregular distributions of the chromosomes it was early shown that a male *D. melanogaster* without a Y chromosome is sterile. Two segments of this chromosome are involved, and both must be present to produce fertility. If one of these segments were translocated to an X chromosome, a race could be established whose X chromosomes both carry the one Y segment, while the other segment remains as a Y (Fig. 114). If this race were crossed with the normal flies, one cross would produce fertile offspring of both sexes; the other reciprocal would produce fertile females but sterile males. Two subspecies of *D. macrospina* show this relation of sterility and sex in their

two reciprocal crosses, but no translocations between Y and X chromosomes have been found in them.

Intersexes. When the normal mechanism of sex determination is disturbed, individuals combining in some degree the characteristics of both sexes may be produced. Such individuals are called *intersexes,* and they are usually sterile. Since intersexes may be the result of hybridization, they are of interest in relation to the isolation of species.
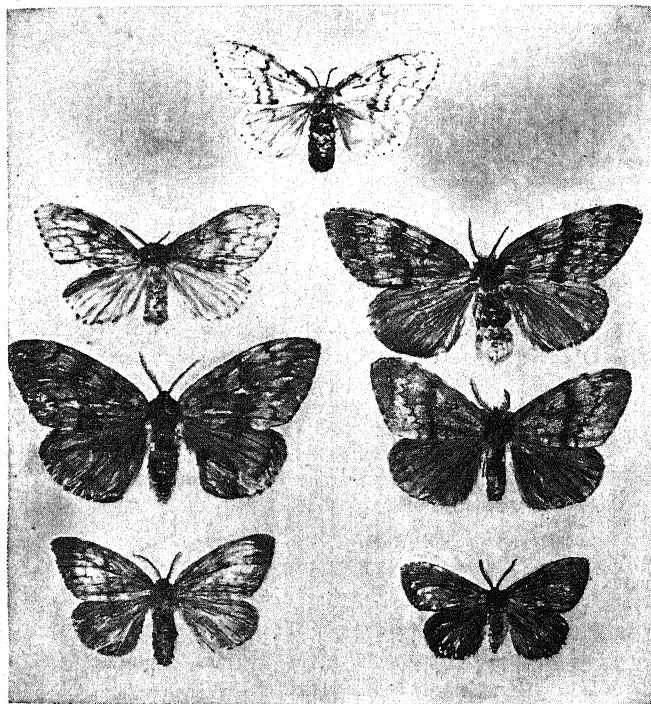
Fig. 115. Intersexes of gypsy moth. Normal female, *above;* various grades of intersex, *below;* and sex-reversed male, *lower right.* (*From Goldschmidt.*)

The best-known intersexes are not species hybrids, but only racial hybrids. They were produced in the gypsy moth by Goldschmidt in a long series of experiments. Moths were obtained from various parts of Europe and Asia and were found to have different sex potencies in different regions.

In moths the male has two Z chromosomes (many geneticists call them X just as in mammals and flies), the female only one, with perhaps a W chromosome (also called Y). The Z chromosomes carry pre-

ponderantly male genes, while femaleness is represented mostly in the cytoplasm. Two male-favoring Z chromosomes in female-favoring cytoplasm produce a male, while if there is only one Z (with or without a W), it is overridden by the cytoplasm and a female results.

Now, Goldschmidt found that races of gypsy moths differ in the "strength" of the male genes in the Z chromosome and of the female influence of the cytoplasm. In some races both Z chromosomes and
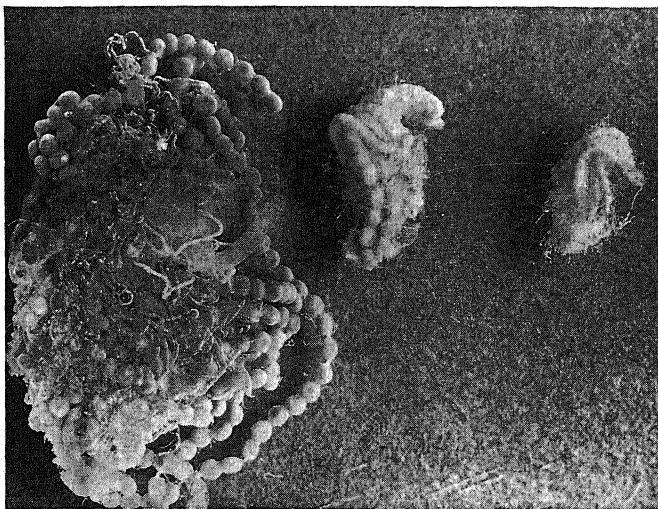
FIG. 116. Reproductive organs of normal female gypsy moth (*left*) and two intersexes. (*From Goldschmidt.*)

cytoplasm are weak; in other races both Z chromosomes and cytoplasm are strong. So long as matings occur only within one race, be it weak or strong, the balance of two Z's or of one Z against the cytoplasm produces clear-cut distinctions between the two sexes. If, however, a strong female is crossed with a weak male, a strong and a weak Z pitted against strong cytoplasm may not produce a male. An intersex may result. And if a strong male is crossed with a weak female, even a single strong Z might overbalance the weak female influence of the cytoplasm, and not a female but an intersex be produced. The sexes differ in wing pattern, size of body, and bushiness of antennae, and of course in their reproductive organs. The intersexes show various intermediacies and combinations (Fig. 115), while their reproductive organs are reduced (Fig. 116).

In general, the races of gypsy moths which lived in neighboring areas

were not sufficiently different in the strength of their sex factors to pro-
duce intersexes on crossing. Races from regions far apart, however,
often yielded intersexes on crossing. There was one exception to this
rule—two neighboring Japanese islands are occupied by races thus
different, but these islands are separated by a wide strait. In natural
situations, therefore, there are not many intersexes. Also, these pop-
ulations are not different species, merely races. Nevertheless, the sex
factors could very well be of different strengths in different species,
and this means of isolation is open to them. Sterile intersexes are known
in few other animals, some ducks, body lice, and guinea pigs among
them.

   Elimination of Hybrids without Sterility. Sometimes species hybrids
disappear without, so far as is known, being sterile. What ecologists
have regarded as an instance of such elimination is found in the hybrids
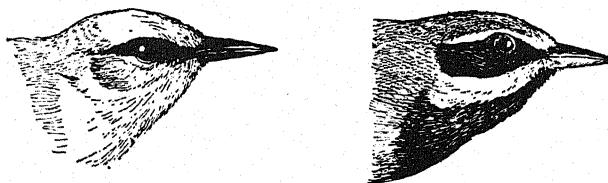
Fig. 117. Blue-winged (*left*) and golden-winged warbler. (*From Chapman, Hand-
book of Birds, Appleton-Century-Crofts, Inc.*)

of the blue-winged and golden-winged warblers (Fig. 117). The blue-
wing breeds in bushy low pastures in a northern range, the golden-
wing in uplands and oak woods to the south. They overlap in river val-
leys of Wisconsin, New Jersey, New York, and Connecticut. The species
differ in appearance chiefly in the color of the under parts, whitish and
yellowish, and the color of the throat, plain or black. These color char-
acters segregate so cleanly that they are regarded as simple genetic
units, with white under parts and plain throat dominant. The bluewing
has one of the dominants (plain throat), the goldenwing the other dom-
inant (whitish under parts). The throat color may just possibly not be
quite so simple; it could be the product of two genes.

   In the regions of overlap there are birds with both dominant char-
acters. They are regarded as hybrids and are called Brewster's warbler.
They must breed together, for occasionally birds with the two recessive
characters are found; these are known as Lawrence's warbler. The
double recessive is understandably much rarer than the double dom-
inant. Backcrosses to the parent types are also known.

Neither of these hybrid types is very common. Certainly they have not produced any general invasion of either the blue-winged or the golden-winged species by the genes of the other. The fact that the hybrids must breed together and with the parent species indicates they are not sterile hybrids, though there are grades of sterility in many known hybrids of other animals. Ecologists have generally held that in some way the environment has selected against these hybrid birds. Each species is fitted to its own kind of environment. Even if the hybrids were intermediate in their ecological requirements, so the argument goes, there would not be enough transitional habitat to maintain the intermediate type.

Speciation. It will be noted that, among the agencies which keep species genetically distinct, some are environmental; others are within the organisms. There has been room here for argument as to just when, or whether, a given population has attained the status of a separate species. Dobzhansky has proposed that speciation shall mean only the origin of reproductive isolation. Geneticists seem inclined to adopt that definition. Ecologists, on the contrary, would prefer to let speciation refer to genetic differentiation of two populations that in fact do not interbreed, irrespective of whether they could interbreed if brought together. Two populations in slightly different ecological situations, kept apart because of some physiological difference which fits them for their respective areas, may well develop genetic differences without losing their ability to interbreed. They have lost interbreeding by ecological separation, but have not lost their *capacity* to interbreed. By the ecologists' definition, the two groups may be regarded as separate species; speciation has already occurred. By the reproductive-isolation definition they are still one species. The latter definition has the advantage of relying on one criterion, though grades of reproductive isolation will still lead to disagreement as to whether, in specific instances, speciation has yet occurred. The word speciation, as a name for reproductive isolation, is somewhat unfortunate in containing within itself so little indication of what it is made to mean.

Choice of a definition here should probably depend on what one wants a definition to do. If the prime requirement be ease and sureness of application, the single criterion would probably be best. Linnaeus used arbitrary criteria, such as numbers of stamens, to distinguish taxonomic groups, but in doing so brought together some plants which by modern standards are not closely related. A nonbiological example may also be useful. A bungalow without a roof would hardly be called a house; it might be called a court or, if it had no floor, perhaps a patio.

Possibly a roof, supported by posts but no walls, would also be called a house. If so, the sharp definition of "house" would be "a roof." Yet if walls were subsequently built under the post-supported roof, the name "house" would doubtless be applied to the whole structure, including the walls. So it could be argued that, though speciation has not been completed until there is reproductive isolation, any genetic differentiation between the isolated groups would still be part of the speciation process. Such differentiation could happen either before or after the reproductive isolation arose. If speciation is to include the genetic differentiation arising before reproductive isolation, it should probably include any that arises after reproductive isolation. By this definition, speciation would be more or less continuous. Usage will decide what meaning is to be attached to the word; but if what happens is understood, names will not be too important.

How long two separated populations could continue to be, and to become, genetically different while still retaining the capacity to interbreed is a matter of some importance. The time was when intersterility was supposed to result from accumulation of genetic differences of any kind whatever. Even now it is sometimes said, though rarely, that two populations become different in so many respects that they can no longer interbreed—the implication being that any mutation in one which does not occur in the other contributes its mite to reproductive isolation. If the only source of reproductive isolation were the failure of chromosomes to pair in the mature species hybrid, the presence of different forms of genes in the parental chromosomes might favor such a failure to pair. But as we have seen, most hybrid sterility in animals is genic, not chromosomal; and there are many earlier points where the interflow of genes may be stopped. There is a fundamental genetic concept which might be held to support the idea that all kinds of mutation contribute to isolation: it is that no gene produces a character by itself; it always cooperates with other genes; indeed it may interact with the whole genotype. Despite this truth, each mutation affects certain features of an organism more than it affects others. In this sense there are still genes for eye color, genes for growth, genes for this or that specific physiological activity. It seems unlikely that all these genes relate in an important way to reproduction.

Many of the visible mutations of Drosophila have, by suitable crosses, been collected into one stock of flies. This stock is enough different from the wild type to be considered a different species if only it were reproductively isolated from the wild type. But it is not so iso-

lated; it is perfectly fertile in crosses with normal flies. The collected mutations have not contributed to isolation.

In nature, however, Drosophila species are reproductively isolated while exhibiting very slight visible differences. Species' distinctions are notoriously small in these flies. Many times have two species been regarded as one until, in breeding experiments, their reproductive separation has been demonstrated. Reproductive isolation is being produced at a high rate, relative to detectable changes of other kinds. It may possibly be said that we do not know all the physiological mutations which are occurring, and that they all may be contributing, in crosses, to reproductive isolation. This suggestion need not be rejected as an attempt to rescue the preconceived idea that all variation helps to create reproductive isolation; it is answered by the fact that Drosophila's visible mutations, which like all characters are also physiological, demonstrably do not contribute to isolation.

It seems necessary to conclude, then, that some mutations, in combination, help to produce reproductive isolation, and others do not. Drosophila appears to be producing the former kind rather rapidly. Reproductive isolation may occur before many other types of differentiation have arisen. Theoretically it could arise before *any* other differentiation has occurred. Reproductive isolation *could* be the *only* distinction between species.

Spatial Separation before Reproductive Isolation. There are strong theoretical reasons for supposing that genes which, on interacting, produce reproductive disturbance must arise far apart if they are to effect isolation. They must arise in separate populations. There need be no barrier separating these populations; they could be parts of the same species and genetically alike, but at distant parts of the range.

To illustrate the argument, it may be assumed that only two dominant complementary genes are involved. They are of the sort which, if one existed harmlessly in one population, the other harmlessly in another population, would if brought together in a hybrid interact to derange the reproductive process. Assume that one of these already exists and has already spread through an entire breeding population. If, now, the second complementary gene arises in the same population, the individual bearing both dominant genes would be at once sterile. To ease this handicap, suppose that the first dominant gene has not spread through the entire population but that it is common. If the second dominant gene then arises in an individual not carrying the first, the heterozygous mutant would be fertile; and if it mates with another

individual not possessing either of the dominants, it will have fertile offspring. The half of its offspring which carried the new dominant would be able to breed with others like themselves or with individuals not carrying either dominant. Random matings would of course lead to unions of both dominants, and some sterility would follow. This loss of individuals would be a handicap to both dominant genes; selection would work against the success of both in the same population. If the effects of the two dominant genes on reproduction were less drastic, so that sterility would be incomplete, both genes *could* become established, but natural selection would still operate strongly against their success.

It is assumed, therefore, that such isolating genes or sets of genes arise separately. At distant points in the range the genetic make-up of the population may be somewhat different, even if only because of genetic drift. If one population occupies a slightly different ecological niche, there is more reason for genetic difference. Thus there may already be some differentiation of characters having no relation to reproduction before the reproductive isolation occurs. The complementary isolating genes are not any more likely to arise *because* there has been other differentiation first; it is merely that populations at a distance from one another can hardly, as a random matter, be identical.

Advantage of Isolation. So widespread is the reproductive isolation of species—fully interfertile species are uncommon—that most evolutionists have concluded that there must be some advantage in the system. They hold that it must have developed under the guidance of natural selection. This would mean that populations cut off from the supply of one another's genes must have left more descendants than did populations which intermingled and interbred freely. Since ultimately it is individuals which produce descendants, those which could breed with other individuals like themselves, but not with others differing from themselves in some group of characters, left more descendants than did those which could breed with different kinds. Wherein lies the advantage of this reproductive isolation?

The answer is that there is need of a certain amount of conservatism in evolution. Gains once made must be held. Recombination, even with the brakes that chromosomes put upon it, could supply organisms with far more readjustment than their slowly changing environment demands. Not only does environment demand no more than slow change: it even penalizes too rapid change. An organism that produces too many kinds of offspring sees most of them rejected. Instead of the dozen types of environment which those offspring would be fitted to enter, there is

usually only one environment. The offspring that were ready to try something new are lost. In the next generation, the ones which conservatively imitated their parents, and so survived, are a larger fraction of the total population. The place of their experimenting fellows is taken by the unchanged or less changed progeny of other parents—parents which did not provide them the means of making many new combinations.

One way to reduce the variability of progeny is to limit the mating of parents to individuals more or less like themselves. If such limitation is desirable, as pictured above, any individual which has developed an isolation mechanism preventing its breeding with distinctly unlike organisms will furnish the unchanged type of offspring which the unchanged environment can accommodate. These offspring will survive, carrying with them their isolation mechanism. If the advantage is real, the selection may be expected to continue until the isolation device is a characteristic of the whole group. Artificial elimination of hybrids of *Drosophila pseudoobscura* and *D. persimilis,* in experiments by Koopman, was followed by reduced frequency of hybrids, which is interpreted as supported for the view that, once a degree of reproductive isolation arises, it may be increased by selection.

Such isolation could be carried too far. Sometime a change of environment will call for a new type of organism, and enough variation must be available to make the adjustment. Isolation must not, then, set aside a population which is wholly uniform; any specific step toward isolation of such a group would presumably be nullified, perhaps long after, by destruction of the population. Nothing is designing these steps; they are all trial and error. What seems an advantageous procedure now may prove fifty generations hence to have been a mistake. By that time the better alternative, which could have been "chosen" fifty generations earlier, may no longer be available. Some mistakes are doubtless irrevocable. That is the way natural selection must work.

This adaptive picture of reproductive isolation is the one that most evolutionists now paint. Some evolutionists base it on the thesis that environments are rather sharply defined, that habitats do not merge gradually into one another. If species did cross, a population possessing an intermediate group of characteristics would presumably result, and an intermediate environment would be needed to accommodate it. If there never had been any isolation, the variation of organisms would spread over the entire range which their various genes could provide. There would be no gaps separating one moderately variable group

from another moderately variable group. The environment, to fit such organisms, would have to display all grades of its various components in all combinations. This, these evolutionists say, environment does not do.

To what extent environment actually falls into distinct types, unconnected by gradations, is of some importance in connection with the supposed origin of isolation. With respect to temperature, environment *does* supply intermediate situations. No area of one temperature, or range of temperatures, is sharply marked off from another area having another temperature or range. There are always intergradations, and these are found in areas large enough to accommodate large populations of organisms. Atmospheric moisture is likewise graded. While it is subject to great temporal variation, so that only averages may be compared, regions of dry air are not sharply separated from moist situations. At the earth's surface, bodies of water do give over suddenly, at the water's edge, to dry land. Yet in Michigan, north of the terminal moraine, there are abundant swamps and marshes furnishing almost any gradation of the water-land contrast. These water gradations are much less extensive, however, than the temperature gradations. Organisms requiring merely damp situations would have smaller choice. No adequate study has been made of all the components of environment, to determine how sharp the areal separations are. What ecologists call "niches" have not usually been demonstrated to be the sharp-angled recesses which the appellation seems to imply. They could often be only "undulations," or at best "scallops," so far as actual ecological measurements show. Perhaps we think of them as niches because we see definite animal or plant types occupying them. If we *should* be reasoning from organisms to habitats, the adaptiveness of reproductive isolation might prove to be an illusion.

It is thus possible to argue on both sides of the question whether, or to what extent, reproductive isolation has been produced through selection. Muller is of the opinion that isolation is a by-product of other characters that have been established through selection, though it is not necessary to make it a by-product of *every* character thus evolved. Huxley likewise regards separation of species as being superimposed upon the other evolutionary processes and as having little bearing on them. Isolation, he holds, is an inevitable consequence of evolution, but irrelevant to its main theme. It would be thinkable that in general isolation is useful, but that it has been overdone by living things. Though the parallel is not too close, one may call attention to the part that isolation plays in Wright's computation of opportunities

for evolution. Partial isolation of small populations in a large group is estimated to afford the best opportunity for such change. Wright is postulating the best chance for change by recombination, without considering whether the change so provided might be too rapid for the change of the environment. Also, the isolation he postulates is not reproductive; it is merely spatial. Were the isolation complete, it would nullify any advantage of having the small differentiated populations. The suggestion has been made that complete reproductive isolation of species might not be the most adaptive arrangement; such isolation might restrict variation too much. Perhaps a small amount of species hybridization would be an advantage.

Anyone who is convinced that every common feature of life on earth has been made what it is by natural selection can point to the occasional species crossing in animals and the more frequent species crossing in plants, and say here is just the right amount of leakage in the isolation of species. An alternative conclusion would be that some things happen that are not particularly beneficial. A result that can be arrived at in many different ways is more likely to be common, and at the same time accidental, than is a consequence of only one kind of event. Reproductive isolation certainly has arisen in many ways. Is its prevalence a consequence of these multiple origins, at least in part, or *must* it be advantageous in order to be so common?

GEOGRAPHIC RACES AND SPECIATION

> . . . geographic variation not merely helps in producing dif-
> ferences, but . . . many of these differences . . . are potential
> isolating mechanisms. . . . Geographic variation is thus capable
> of producing the two components of speciation, divergence and
> discontinuity.
>
> —ERNST MAYR, 1942

If, as must in general be true, the factors of reproductive isolation arise in populations that are already spatially separated, speciation should at least often involve peculiarities of distribution. If one could follow the history of the origin of a species, any discovered features of distribution involved in it should throw considerable light on the nature of the differentiation process. Unfortunately the origin of species, except through polyploidy, is too time-consuming for as short-lived a being as man to witness. While a species could arise in a century, the probable time is much longer, and some evolutionists speak confidently of a million years as a not uncommon requirement. Such lengthy procedures cannot be followed directly.

There are not wanting, however, means of tracing biological processes without watching them happen. While embryonic development of a frog can be followed with ease so far as external changes are concerned, most details of internal procedures are beyond direct observation in a living embryo. But by sectioning successive stages of different embryos and making comparisons between them, the complete story of development is pieced together. After that has been done, an embryonic organ apart from the rest of the body can be assigned to its proper place in the series of events.

It should be similarly possible to learn something about speciation from embryonic species. We do not need to section the developing species; that has been done for us. We see the sections all around us. Merely by living at the present time, we are put in the midst of a collection of such sections. Like the sections of an embryo, the sections

of species have to be interpreted. Unlike those of an embryo, they are not labeled. There is nothing to tell us that this one is a thousand years old, that one has been growing ever since the retreat of the last glacier, another started soon after the Great Lakes settled into approximately their present positions. Their ages have to be judged by their present condition, the probable history of their environment, and the nature of the populations around them.

Success in making the necessary interpretations is certain to be variable. In the view of some evolutionists, such interpretations are bound to fail. Conceiving the things we are about to study as sections of species in the making implies that speciation is a gradual process; and Goldschmidt regards species making as a sudden event. Only a "systemic mutation," he holds, can originate a species. Such a mutation is held to change radically the whole genetic mechanism. Other evolutionists, looking diligently for systemic mutations, find only one close approach to them, polyploidy, and it is clear that animals have made little use of this means of speciation.

Accordingly we shall adopt the prevailing view that species formation is a gradual process and that geographic distribution has a bearing on it. That procedure would not be invalidated even if some of the geographic races to be examined should never become species. If such races have been doing the things that species do in becoming species, they are informative even though they do not complete the process. A traveler flying west with the intention of going to Seattle is on his way to that city. He may never arrive because his plane crashes in the mountains; but up to that moment he was on his way to Seattle. His purchasing a ticket and boarding a plane indicate the way of going about arriving at a distant place.

Geographic Variation. The mere fact of geographic variation is revealed by any extensive taxonomic work on almost any group. Very few species are uniform throughout their range. If one were to make appropriate genetic tests, it would probably be found that every breeding population differs from every other breeding population; percentages of alternative genes provide the fine gradations which such a distinction would require. As a practical matter, however, one has to limit geographic contrasts to things that can reasonably be detected— usually, though not always, things that can be seen.

On a very local scale wild Iris, as studied by Anderson, shows different characters in different places. These plants grow in isolated colonies, some consisting of only one plant (including the vegetatively produced branches of the rhizome which by decay may become sepa-

rate), some containing several thousand individuals. A single plant may cover several square feet, or rarely several acres. The plants differ in color patches on the petals, floppiness or erectness of the petals and sepals, and other features. The colonies, even the nearest ones, usually differ in their combinations of these characters. In southern Michigan, north of the terminal moraine where swamps are common, these colonies would, if uniformly spread and arranged in the most compact plan, be rather more than half a mile apart (Fig. 118). In Alabama, colonies would average 4 or 5 miles apart, with about the same degrees of difference as in Michigan.

FIG. 118. Areas occupied by colonies of *Iris virginica Shrevei* in a 50-square-mile region around Schoolcraft, Michigan. (*After Anderson.*)

The gypsy moth has already been mentioned as having different strengths of the sex factors in different areas of Europe and Asia. The races of Europe are mostly weak, those of continental Asia mostly medium, and those of the principal Japanese island strong; yet another Japanese island has the weakest of all the races. Other features in which the gypsy-moth races differ are the length of time of larval development, the number of molts the larvae undergo, the color of the larvae, etc.

Snails of the genus Partula may be either dextral or sinistral. Within a single species the frequencies of the two types on the island of Moorea range from all dextral in some valleys, through various mixtures in other valleys, to all sinistral in still others. The blood-cell antigens of man change in frequency, A increasing from south to north in native Indians of western North America and from north to south in the Malay Archipelago and Australia, while B increases from Europe eastward and from Australia northward to eastern Asia. The lady beetle Harmonia has spots of very variable size. In any one population these spots show sizes distributed according to the normal probability curve; but the mean size is small in central and southwestern Asia, larger in western Europe and eastern continental Asia, and still larger on the Japanese islands.

In the Solomon Islands, birds of one species (*Pachycephala pectoralis*) are divided into several groups occupying different islands or groups of islands. Males have white throats in one of these areas, yellow throats in several others, intermediate in two. The females are grayish-olive in one area, bright orange with a brownish wash in another, pale gray with a brownish wash in a third.
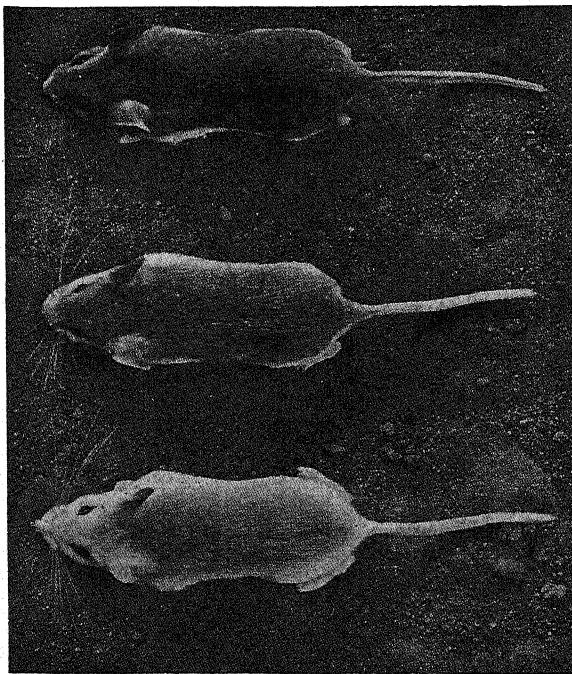
FIG. 119. Three subspecies of *Peromyscus polionotus* on dark soil. *Above*, subspecies *polionotus; middle, albifrons; below, leucocephalus.* (*From Sumner in Bibliographia Genetica.*)

Bird songs sometimes differ geographically. A species of bunting in Central and South America has several different songs, with a specially different one on the island of Santo Domingo. The Spanish race of the chiffchaff has a song so different from that of other European races of the species that it is more like another species of the same genus (*Phylloscopus*). In this same genus, in the Malay Archipelago, the song is quite constant in each species while the color, pattern, and size vary geographically. Song is thus variable in southwestern Europe, stable from New Guinea to the Solomon Islands.

Migratory habits of bird species sometimes differs in different races. The bunting whose song varies (see above) is sedentary except in one Patagonian race, which migrates. A species of hummingbird has one race which stays throughout the year on the islands of Santa Barbara and San Clemente off the coast of California, but another race on the mainland which migrates to Mexico in winter.

The list of geographic differences could be extended almost without limit. In birds, the best-known taxonomically of all the animal groups, there is said to be geographic variation in every character that distinguishes one species from its nearest relatives. Enough differences are known in other groups to show that they constitute a very common feature of species. Many more examples will appear in the following sections, where geographic variation is examined for features that are pertinent to the speciation process.

Adaptiveness of Geographic Races. While species characters have not often been definitely shown to be adaptive, some of them may be. It is accordingly of interest to point out areal races which are known to be, or suspected of being, distinguished by useful properties. The gypsy-moth races are adapted to the temperature of the regions where they exist by having a speed of development which leads their larvae to emerge at the right time in the spring. It might be fatal to hatch before the proper food was present or after its most suitable stage had passed.

Among mice, color related to the background is known to be a protection in some instances. Three races of the deer mouse *Peromyscus polionotus* are so located as to be rendered less conspicuous; *leucocephalus,* the palest, lives in areas of white sand, *polionotus* in regions of dark soil, and *albifrons* on intermediate background. Seeing all three together on dark soil (Fig. 119) and on light sand (Fig. 120) is convincing evidence that conspicuousness does depend on their color in relation to the soil. In view of the experiments of Dice and others on protective coloration, it seems likely that these three subspecies gain by their similarity to the surroundings.

There has been a tendency to offer the same explanation—the advantage of inconspicuousness—for the paleness of mammals in dry regions, darkness in humid regions. Moist regions, it is pointed out, are darker, and in general the mammals are darker there. This explanation is weakened by the fact that bats, which are not exposed on soil as a background, and birds which live in bushes or trees, not on the ground, are also darker in moist regions. These latter differences suggest that something more than visible contrast, and the eyes of predators, is

involved. Climate furnishes so many factors besides shades and colors that a more complex relation seems a possibility. In *P. maniculatus,* one subspecies lives in a moist coastal area, another in a high desert. The former is dark, the latter pale. The thyroid glands of specimens which had been kept in the laboratory for several weeks on the same diet showed the differences in structure indicated in Fig. 121. What these differences mean is uncertain, but there is room to suppose that some-
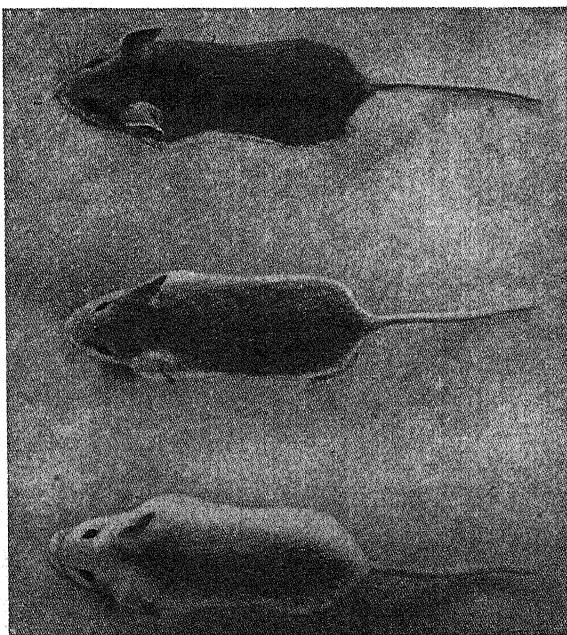
FIG. 120. The same subspecies of *Peromyscus polionotus* as those of Fig. 119 but on white sand. (*From Sumner in Bibliographia Genetica.*)

thing else than predators' eyes may furnish the selection. There is no way of knowing whether the thyroid differences are adaptive or not.

Ecological Rules. Possibly related to the question of adaptiveness, as discussed in connection with moist and dry climate and the color of mammals and birds, is a group of ecological rules applicable to certain vertebrate animals. It is generally true that races of mammals or birds living in cool climates are larger than races of the same species living in warmer regions. Certain burrowing animals furnish an exception to the rule. Another generalization is that protruding structures—tails, legs, ears, beaks—are shorter in cooler than in warmer parts of

the species range. According to still another rule, dark colors tend to prevail in warm, humid regions. Arid regions are marked more by reds and yellow-browns. This rule applies to a number of insects, not just to the warm-blooded vertebrates.
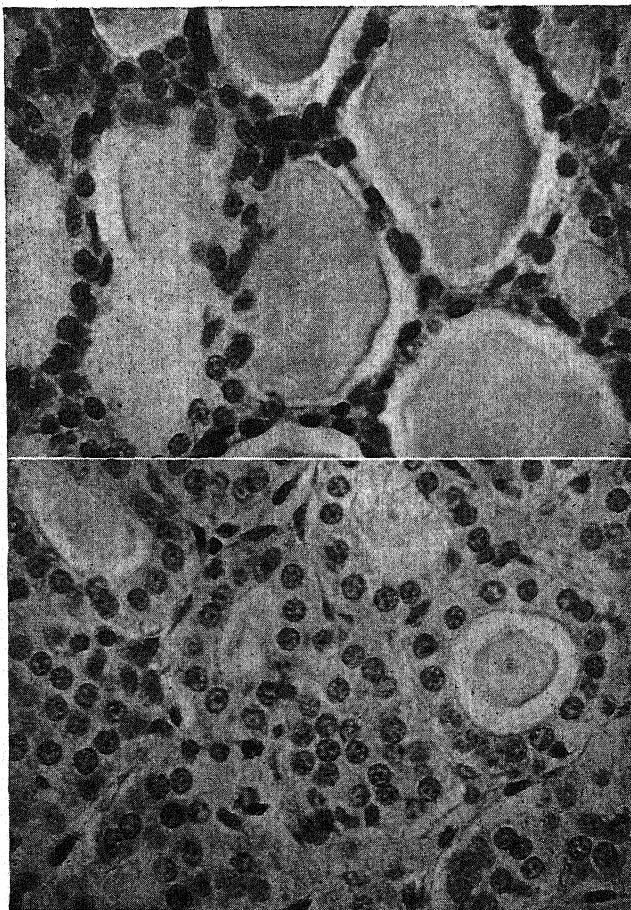
Fig. 121. Follicles of thyroid gland of mouse *Peromyscus maniculatus*. *Above,* dark coastal subspecies; *below,* pale subspecies of the desert. (*From Yocom and Huestis in Anatomical Record.*)

The fact that such rules are supported in a general way by facts, even with exceptions, leads to the suggestion that they rest on natural selection and that the characters to which they relate are adaptive in the regions where they are found. The belief is not based on any

specific advantage which the thing we see could confer on its possessor. Under these circumstances, the selective advantage must lie in the physiological constitution that produces size or color, not in the size or color as such. There are other rules for mammals only, or birds only, or for snails. To state them all would lead us too far; our interest is in the possibility that they afford evidence of unrecognized adaptive features.

Geographic Races Genetically Distinguished. The possibility of relating some geographic races to the nature of the environment led early to the supposition that the "racial" distinctions might be phenotypic, that is, merely changes in the expression of the genes as these had to respond to other environments. Were this the explanation of such areal differences, evolutionists would not be concerned with them. Any doubt on this score has been removed in a few instances. Sumner, after demonstrating geographic differences in mice, brought members of the contrasted groups into the laboratory where they were maintained for several generations under identical conditions. The groups maintained their distinctions, which could thus only be genetic in origin. No two of the races tested differed by just one gene; they were all more complicated than that. This is the more striking evidence because Sumner, in his earlier experiments, had amply demonstrated that environmental factors, particularly temperature, do modify these mice. Dice has also shown, by laboratory breeding, that geographic differences in mice are genetic. Even within one geographic race (subspecies) he found that gray and buff color differ by more than one gene, so the characters involved are not simple.

The gypsy-moth races were also shown by Goldschmidt to be genetically distinguished. Besides the speed of development, number of larval molts, strength of sex factors, and color of the larvae, the genetic distinctions include size of body and resistance to infectious disease. Many groups of Drosophila from different areas have been shown to differ in the frequencies of chromosome inversions or mutant genes. Genetically well-known forms are particularly suitable for demonstrating geographic distinctions of this statistical kind, where phenotypic differences were not first observed.

In the lady beetle *Hippodamia quinquesignata* (Fig. 85), whose typical banded pattern is found in the Rocky Mountains and westward to about the middle of Washington and Oregon, there is a spotless subspecies (*ambigua*) replacing it through the western half or third of these two states (Fig. 122). There are occasional spotless individuals in the area of typical banded *quinquesignata,* and these have been

demonstrated, in crosses, to owe their spotlessness to a single domi-
nant gene. It seems almost certain that the pattern of the subspecies
ambigua is dependent on this one gene, though no cross has been made
between a spotless beetle taken within the *ambigua* area and a banded
one from the eastern part of the range. The two subspecies are identi-
cal with respect to the male genitalia, on which taxonomists rely heav-
ily in classification, and a spotless beetle with these genitalia would
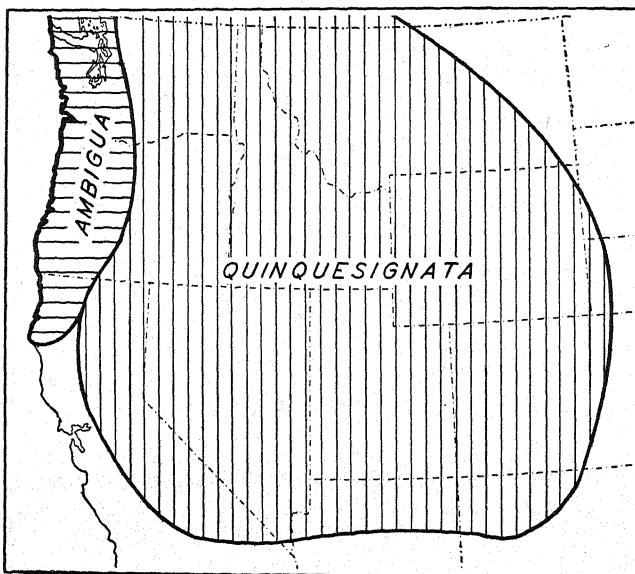
Fig. 122. Approximate range of lady beetle *Hippodamia quinquesignata* with its
spotless subspecies *ambigua*.

undoubtedly be called *ambigua* unless its locality label indicated that
it was collected outside the area where the spotless race prevails.

Aside from actual crosses, there are ways of judging, subject to some
error, whether geographic groups are separated by genes, or only by
phenotypic responses to environment. Genetic differences are more apt
to be sharp. Two populations may differ only in the frequencies of
certain genes (and hence usually characters), while the individuals
that show the contrasted characters are sharply different. Individual
responses of the same genes to different environments could be sharply
different only if there were sharply defined thresholds in the physiology
of development. Without such thresholds, phenotypic response should
change more gradually. This criterion does not detect all genetic

groups, because some genetic characters are dependent on a number of cumulative genes, and such characters should present gradations of expression in individuals. It is only simple characters, or those with a genetic threshold of expression, that should be sharply different in individuals. Another likely distinction between genetic and environmental geographic distinctions is in the area covered and the continuity of them. A genetically distinct group is likely to cover a considerable area which includes several kinds of habitats. A group responding to environment is likely to be in small areas, which are duplicated here and there as the same combinations of conditions are provided.

Applying such tests as the two above to geographically different populations leads to a great increase in the list of such populations that must be regarded as genetic. Indeed, most groups to which the term "race" could be even hesitantly given must merit that name on the ground that they are genetic. This does not mean that there are few ecological races. There may -be many races which are ecological, though probably not so many as numerous ecologists have supposed. They are ecological, however, in a selective sense. Environment has not *produced* the difference of a group that may be called a race. Almost certainly it has not modified the genes; it has only sifted them. Nor are geographic races necessarily to be distinguished from ecological ones. A race may be both. Indeed, Mayr holds that every geographic race *is* ecological to some degree.

Clines. Pursuit of the idea that geographic variation may be part of the process of speciation requires consideration of the ways in which races are separated or connected. In many instances there is a gradual change from one place to a distant one; a gene frequency changes little by little; a character·changes by small gradations; the number of individuals exhibiting a character increases or diminishes in a given direction. Such gradations are called *clines* by Huxley, and he lists many of them. Some clines may be responses—selective ones—to a graduated environment. Probably more of them represent the extent of spread of new genes from their point of origin, carrying with them a gradation of the characters they help produce, the details depending on how the characters are inherited. Usually the ecological or genetic basis of particular clines is unknown.

The bird of paradise in eastern New Guinea presents two of these clines, one affecting the color of the back, the other the color of the plumes (flank feathers). South of the uninhabitable mountains forming the backbone of the island (Fig. 123), the entire back is brown; northeast of the mountains the whole back is yellow; and at the tip of

the island the upper part of the back is yellow, the lower part brown. The plumes are red over most of the range of the species, that is, all along the south side of the island, around the tip, and up along the northeast coast. At the other extreme of the range the plumes are all orange, and between the two areas is one of orange-red plumes. The points of mixture come at different places for the two characters, so that five different combinations of back and plume colors exist. The
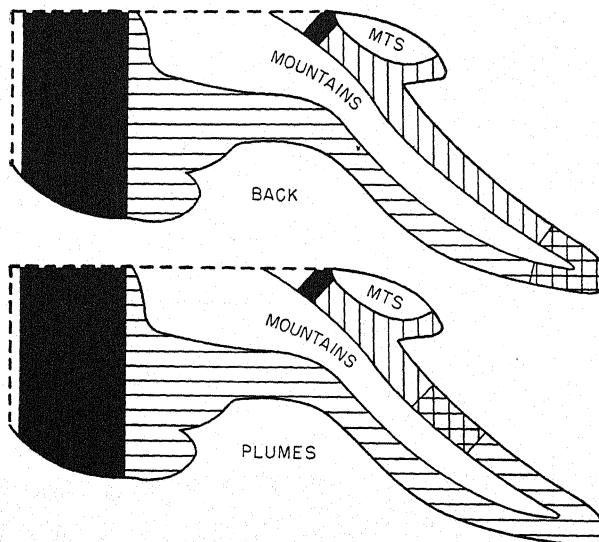
Fig. 123. Schematic maps of southeastern New Guinea showing two independent clines of the bird of paradise. *Above*, horizontal shading, back all brown; vertical shading, back all yellow; crosshatching, upper back yellow, lower back brown. *Below*, horizontal shading, plumes red; vertical shading, plumes orange; crosshatching, plumes orange-red. Black, areas of hybridization with two other species. (*After Mayr*.)

birds in these groups are recognized as five different subspecies. No gradient of the environment appears to fit these color gradients.

There is no reproductive isolation in these clines; that is why they are still clines. If such isolation should arise, there is little doubt that the fine gradation would yield to a gap. When Mayr points out that where there are many clines there is little speciation, he is presumably only saying that clines can exist only while there is no isolation. Genetic differentiation on a geographic basis but with graduated change does not produce species. Yet, if isolation should later occur, the preceding differentiation might well be regarded as part of the speciation

process. Clines *could* be on their way to producing species, but the critical isolation would have to follow.

Isolation in Geographic Races. If geographic races are sections of embryonic species, as they were pictured as very possibly being in the opening paragraphs of this chapter, study of numerous races should reveal some with at least traces of reproductive isolation from other races. Such races would be the late embryos of species—correctly so portrayed even if they should die *in utero.*

Sumner described a situation in the mouse *Peromyscus polionotus* which some evolutionists might consider early isolation, though Sumner himself rejected that view. These mice have already been described (Figs. 119 and 120) as examples of protective color (adaptiveness of races). The pale subspecies *albifrons* is found from the Gulf Coast northward, steadily but very slowly becoming darker, for a distance of about 40 miles. Then in a strip less than 10 miles wide (Fig. 124) it becomes rapidly darker. At the northern limit of this strip the mice are almost as dark as the subspecies *polionotus.* From there on inland for about 50 miles more the color very slowly darkens, though all through this 50-mile area the mice would be definitely

FIG. 124. Part of the range of a Peromyscus species showing sharp transition between the subspecies *albifrons* and *polionotus.*

classified as *polionotus.* Sumner rejects the idea that *albifrons* and *polionotus* were earlier definitely isolated and have now come back into contact, with resultant hybridization. Yet the 10-mile transitional strip is just what a degree of isolation should produce, and there is no known feature of the environment—certainly not the color of the soil —which changes just where the mice change. The subspecies have been crossed in the laboratory, but not enough was discovered about their genetics to explain the strip of rapid transition. Sumner suggests that there may be assortative mating or that hybrids are less successful in both ranges than the respective pure subspecies are. The former

would be a sort of ethological isolation, the latter a selective isolation.

Two subspecies of *P. maniculatus*, one a prairie form, the other living in forests, meet in one small area in Glacier National Park without hybridizing. This is judged principally from tail measurements. While the tail of one may rarely reach 90 mm. in length, the tail of the other is seldom so short. There are practically no individuals having the crucial intermediate tail measurement. The area in which the two subspecies meet is small, which raises the question whether they may not be spatially isolated despite what appears to be an overlap. This situation is discussed again in the next section.

Frequently it is impossible to tell, from the characters of individuals, whether there is reproductive—or other biological—isolation between subspecies or not. In birds it is usually not possible to apply the test of laboratory crossing. The great white heron of the Florida Keys is usually regarded as a separate species, but Mayr suspects it is only a color mutant of the great blue heron that has, perhaps accidentally, come to be the only representative of the species in the Keys area.

Races of gypsy moths show some isolation, though most often not between adjacent ones, by producing intersex (hence sterile) hybrids. They are also kept apart spatially by temperature preferences. Such habitat preferences could be the start of more obviously genetic isolation. A thrush species on the main Japanese islands is divided into two races, one which lives at an elevation of a thousand meters and nests on the ground, and another at sea level nesting in hollow trees about 3 m. above the ground. A species of Japanese warbler is divided into two races, differing in that one nests on the ground, the other in bushes; also they sing different songs. The two races live in different parts of the archipelago. Half a dozen species of birds have each two races, one living at the foot of the Himalaya, the other up the mountains. While isolation of this ecological type is not what the geneticist is looking for as the mark of distinct species, ecological separation should help the factors of reproductive isolation to get established.

In frogs of the species *Rana pipiens* there are races adjusted to different temperatures in the embryonic stage. Naturally these preferences form a north-south gradient. Moore finds that neighboring temperature races can be crossed and produce normal hybrid embryos; but as the distance between their natural habitats increases, the embryonic development of their hybrids becomes more and more abnormal. The extremes of this gradient produce, on crossing, more abnormal embryos than does *R. pipiens* when crossed with three other species.

The 17-year cicada, though maintaining peak years of emergence,

has somehow broken up into groups producing lesser peaks. The immature period is mostly 17 years in northern states, but as low as 13 years in the South. Even in one general region, however, the broods do not emerge in the same year. In West Virginia there are nine independent groups of varying size which reach maturity in different years. Eastern North America in general has comparable strains with differences in numbers and years. The fact that these peaks of emergence have the same rhythm is the evidence that the lines of descent
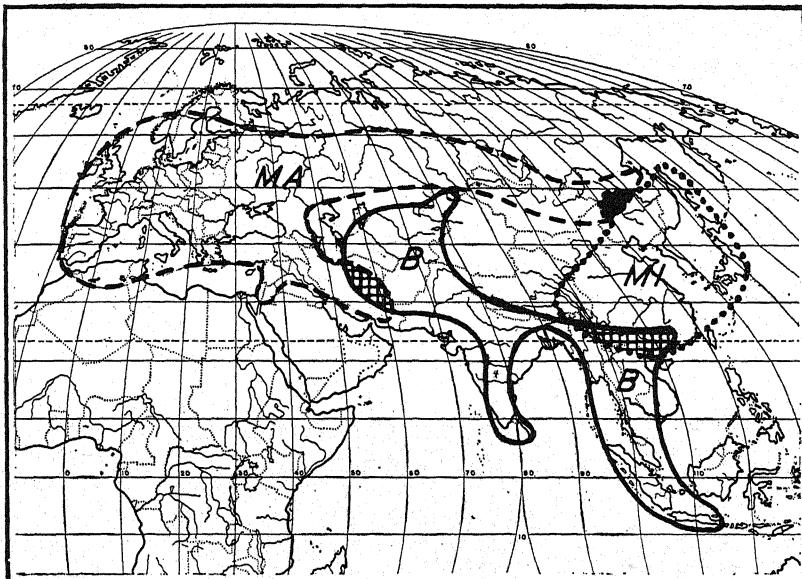
Fig. 125. Ring of subspecies of the titmouse *Parus major*, showing reproductive isolation at one point (black) of overlap, intergrading (crosshatched) at the others. B, subspecies *bokharensis*; MA, *major*; MI, *minor*.

are separate. They are isolated from one another very effectively. Whether they have any reproductive isolation cannot be stated, for they cannot be crossed; but the separation of their years of emergence sets the stage for possible establishment of complementary sets of genes that could result in reproductive isolation. How the lines of descent became separated is unknown. It must have been through some speed-up or retardation of development in some members of the species. Morphologically the strains are all alike; isolation has not produced any differentiation.

It is questionable whether *Drosophila pseudoobscura* and *D. per-*

similis should be mentioned in this discussion. They were formerly regarded as races A and B of *pseudoobscura*. They are reproductively isolated in nature and when crossed in the laboratory produce hybrids that are sterile in the male sex. They are phenotypically practically identical, and even after their isolation was proved there was difference of opinion as to the taxonomic status that should be assigned to them. Were they still embryonic species, or had they already been born? Dobzhansky finally decided they merited specific rank and gave race B the name *D. persimilis*. Geneticists have mostly followed him, but there is one eminent exception.

Rings of Races. The situation presented by the frog *R. pipiens,* in which abnormality of race-hybrid embryos increases with the distance between the races crossed, has a striking modification in species with rings of races. In the titmouse *Parus major* there are three subspecies. One (*minor*) occupies Japan and the eastern part of the mainland of Asia down to southern China. Here it intergrades by hybridization with a second subspecies (*bokharensis*) that extends westward to the Caspian Sea (Fig. 125). Southeast of that sea it merges gradually with the third subspecies (*major*), which occupies Asia Minor and most of Europe and extends across Siberia. At the eastern end of this last range *major* meets and overlaps with *minor* without hybridization. These two subspecies are isolated reproductively, while each of them crosses readily with *bokharensis*. But for the existence of *bokharensis*, the subspecies *major* and *minor* would be regarded as distinct species.

The warbler *Phylloscopus trochiloides* is broken up into five subspecies. Subspecies *viridanus* stretches from the upper part of the Yenisei Valley, in southern Siberia (Fig. 126), southwest into Afghanistan, and into Kashmir. There it intergrades by hybridization with a small subspecies *ludlowi* which is practically limited to Kashmir. This in turn intergrades with *trochiloides* which extends along the southern border of Tibet and through Nepal into China. There *trochiloides* meets *obscuratus*, with hybridization, and this merges with *plumbeitarsus* to the north. The last of these subspecies spreads widely through northern Mongolia and Manchuria, and far into Siberia. The western limit of *plumbeitarsus* is in the upper valley of the Yenisei River, where it overlaps the range of *viridanus*—but here without hybridization. Again *plumbeitarsus* and *viridanus* would be regarded as separate species were it not for the three intergrading forms joining them in a ring.

A similar ring is formed by the mouse *Peromyscus maniculatus,* already mentioned as having a prairie and a woodland subspecies which meet in Glacier National Park without hybridization. Both these sub-

species intergrade with a third subspecies south of them, and with still another north of them. There is some ecological separation in the park area of meeting, since one subspecies is a woodland form, the other a prairie form. Yet many another pair of subspecies has intergraded with as much habitat separation as these two have.
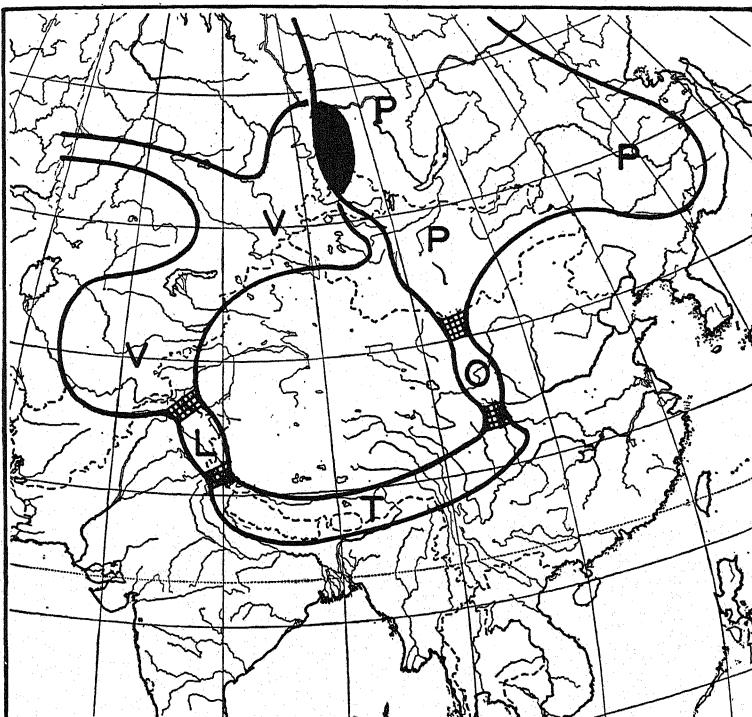
FIG. 126. Ring (semidiagrammatic) of subspecies of the warbler *Phylloscopus trochiloides*, with isolation at one point (black) of overlap, hybridization at four others (crosshatched). L, subspecies *ludlowi;* O, *obscuratus;* P, *plumbeitarsus;* T, *trochiloides;* V, *viridanus.*

Geographic Races and Species. Subspecies and other geographic differentiations exhibit so many grades of the distinctions between uniform populations and separate species that one can hardly avoid the conclusion that they show *one* of the ways in which species have been formed. It seems unlikely that any of the greater degrees of separation which geographic groups present could have been attained without going through the lesser grades. Two subspecies which show mild signs of reproductive isolation are so near to the situation of two distinct

species that it would seem reasonable to suppose that the next step, acquisition of practically complete isolation, was often taken. It appears justifiable to conclude that the spatial separation which accident or external agents provide in geographic races *permits* the establishment of the internal factors of isolation of species, and that reproductive isolation often *has* followed such separation.

CHAPTER XIV

SOCIETIES OF BEASTS AND MEN

> Customs and prohibitions, embodying centuries of accumu-
> lated experience and handed on by social tradition, take the
> place of inherited instincts in facilitating the survival of our
> species.
>
> —GORDON CHILDE, 1936

Because of the extent to which certain kinds of animals have de-
veloped societies, the widespread occurrence of some (often minor)
degree of social behavior in the animal kingdom, and the fact that
one of man's characteristics is a complex social system, it is necessary
to consider these phenomena in terms of evolution. It is particularly
important to indicate what relation they have to biological evolution,
to which this book is devoted. Confusion between evolution resting
on the genetic mechanism and gradual change of other kinds could
lead to serious misunderstanding of both types of evolution. Nothing
short of a review of what man and other animals have done as societies
seems adequate to forestall wrong concepts, though that review need
not be lengthy.

Collections of Animals. As a start, we may look at some of the groups
of animals of the same species whose association either is not under-
stood or hangs on a very tenuous thread. We shall be interested only
in those animals which are brought together because of a relation of
individuals to one another, or which we deem to be collected in this
fashion. Collections of individuals about a localized food supply, such
as is washed up on the shore of a body of water, hardly constitute so-
cieties. Individuals would go to these sources of food, whether other
individuals went there or not. Shelter and a required type of medium
on which to live often entail a grouping of individuals, but quite with-
out social significance. A water hole in the wilderness brings many
kinds of animals together, but only because they all require water and
have discovered where it may be obtained.

The grouping for which we are looking is one in which animals are where they are because others like them are there. Perhaps they are displaying some sort of cooperation, but in the simplest (to us) cases we shall not know. In considering cooperation we shall not go back, as a philosopher might, to the cellular "cooperation" which led to the formation of multicellular animals out of protozoa. For if we did, we might feel it necessary to explain the water in which the protozoa lived as resulting from the cooperation of hydrogen and oxygen—gases which do form water whenever they are brought together under certain conditions. We might also feel impelled to consider the cooperation of two and two in making four as these adhering cells multiplied. The important feature of the early stages of evolution of metazoa seems to be physiological; calling it cooperation is hardly more than pointing out an analogy.

Assemblages of lady beetles in great masses in winter must be something more than meeting physiological requirements in the few places where suitable conditions exist. On chill mornings in the fall great numbers of certain species encrust rocks or logs. Not all suitable rocks are thus covered; the beetles are crowded together on some of them. Other species eventually fill postholes or pile up in grassy places, sometimes on a south slope, offering the suggestion that perhaps warmth is the reward of their behavior. Masses, even of cold-blooded animals, have been shown to maintain temperatures above that of the medium about them. Yet the advantage of massing cannot explain the process of collecting into one place. The beetles do not know about that advantage. Whether they follow leaders, or sense the odor of a collection started arbitrarily or accidentally in some place by a few beetles, or are directed by some other sense is quite unknown. The process must, however, relate the beetles to other beetles of the same kind, for the hibernating masses, with occasional exceptions, are made up entirely of one species.

Insects in flight are sometimes associated in great multitudes. A species of leaf beetle was once observed in such an operation, forming a stream 15 feet deep and 100 yards wide, continuing for two days. Midges put on a much less striking spectacle when the males dance in swarms, "waiting," a human being might say, for the females to come by. Honeybees form clusters in winter, with the result, but hardly the purpose, of maintaining a higher temperature.

A classical example of unexplained group behavior of mammals is the periodic migration of hordes of lemmings. Known for more than a century, these migrations were restudied in 1895 by Collett. The small

mouselike rodents live in the mountains of Norway, near the timber-
line. Ordinarily they produce one or two litters each summer, four or
five young in a litter. At irregular intervals their reproduction is
stepped up to three or four litters a summer, with as many as eleven
at a birth. By August the first litters are themselves producing offspring.
Moreover, at these times they escape serious disease. Great overpopu-
lation is the result, and forced emigration occurs. First, some of them
leave their meadows and take to the forest. The next year their num-
bers may increase still more. They set out in great droves, traveling
west even though that takes them into barren territory. They are preyed
upon by all sorts of rodent-eating birds, but many of them reach the
fiords on the west coast, where they are drowned. The rivers and upper
reaches of the fiords may be nearly filled with their bodies. Some ac-
counts of the lemming migrations state that the animals travel in par-
allel rows, eating their way through the long Norwegian racks of hay
(not equivalent to haystacks in America) and going through streams
in the same rows. Calling these movements an effect of mob psychology
does nothing except recognize the migrations as social behavior. Cer-
tain birds have performed such infrequent migrations, going hundreds
of miles. The meadow mouse in Nevada experienced the great increase
in numbers, again without known explanation, but in them the induced
migration was very short.

Schools of fishes are formed in many species, for no apparent reason
and with no known advantage, though conjectures of benefits have
been made. Conditions of the water in the midst of the school are the
same as between schools, and the assemblages move erratically from
place to place. The only difference between a place occupied by a
school and one not so occupied seems to be that the former has fish in
it, the latter none. The fish are there apparently because other fish
are there.

Brittle stars, those slender-armed relatives of the starfishes, if put
into an otherwise bare aquarium, cling to one another and remain so
bunched for weeks. But put eelgrass or a glass-rod imitation of it into
the aquarium, and the stars disperse and climb over the introduced
scaffolding. The groups were an unnatural product, but the result of a
natural reaction.

Various animals form associations at night. Certain solitary bees form
overnight aggregations of males only. A butterfly species in Florida
collects in the same places night after night. The chattering hordes of
starlings in single trees are a common pest in the early morning.

Migrations of birds are often performed in great masses. The V-

shaped group of geese is relatively small. Advantages of such groups can be imagined, but it is harder to prove them.

Advantages of Grouping. Some assemblages of animals can be shown to be beneficial, and for some of these the source of the advantage may be ascertained. Quails huddle together at night in cold weather, facing
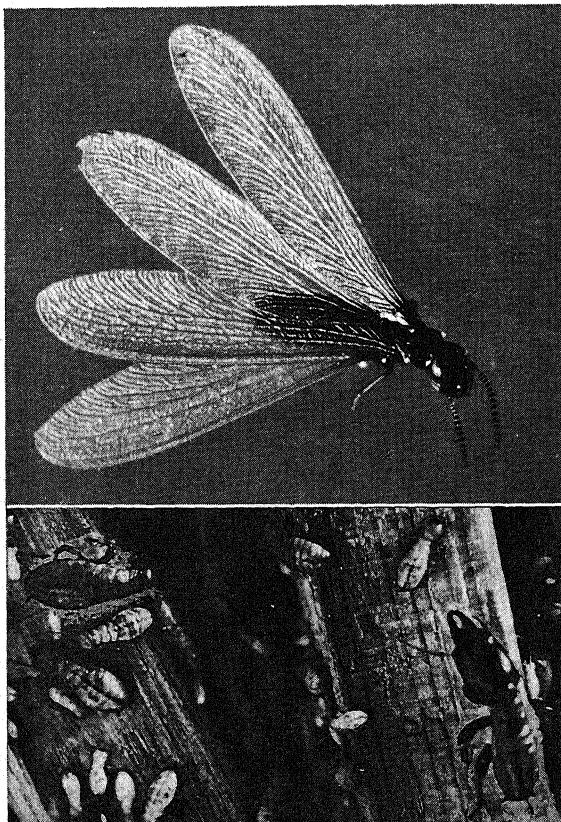
FIG. 127. Termite queen, enlarged; (*below*) soldier (*right*), workers, and immature forms. (*From U.S. Department of Agriculture and Professor E. O. Essig.*)

outward in a circle and sitting wing to wing. In severe weather the covey may be two-storied, some birds perching on the backs of others. Conservation of heat in this manner has been shown to save some lives. Pronghorn antelopes of the western prairies behave differently under attack by wolves or coyotes, depending on how many of them are together. If a dozen or more are in a group, they make a stand, and the

bucks fight off the enemy. Fewer than a dozen do not make this group effort, but scatter, and the slowest runners are usually killed.

One clear instance of an advantageous social group is the termite colony. These insects (Fig. 127) are essentially wood eaters; yet they are themselves unable to digest cellulose. They have to have this digestion done for them by hordes of flagellate protozoa (Fig. 128) which live in the termites' intestinal tract. Now, at every molt the termites lose their protozoa and have to be reinfected from other termites. It would
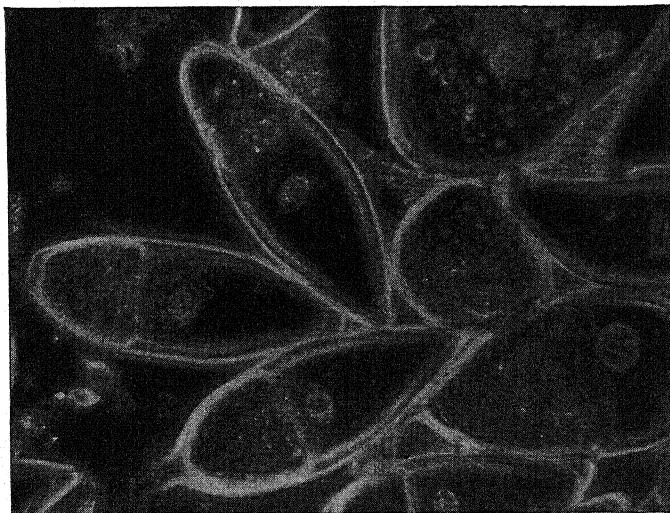
Fig. 128. Flagellate protozoon which inhabits the intestines of termites of one species and digests cellulose for them. (*Courtesy of Professor Harold Kirby.*)

be fatal for the termites to lead solitary lives, for they would soon starve to death. Termites have several morphologically different castes, as is pointed out later. Only one of these castes is reproductive. When a pair of reproductive individuals moves away to found a new colony, it is essential that they be already infected with the protozoa.

The size of a group is sometimes important in relation to the benefits of grouping. For two species of gulls it has been shown that eggs are laid earlier if the group of birds is large. There must be some stimulus to laying which other birds provide. Also, the eggs are laid faster, making the laying season shorter, if many individuals are present. This concentration of the breeding season proves to be useful; more of the young survive. Small collections of terns are less successful than large ones, probably because only a large group can make enough disturb-

ance to frighten the pillaging gulls away from their nests. The larger colonies of yellow-headed blackbirds are the most successful ones. Fulmars (birds) require about four years after they have occupied a new area before egg laying starts. The smallness of the group making the new settlement in some way postpones egg laying. Elephants are said to require at least twenty-five members of a group if they are to maintain themselves.
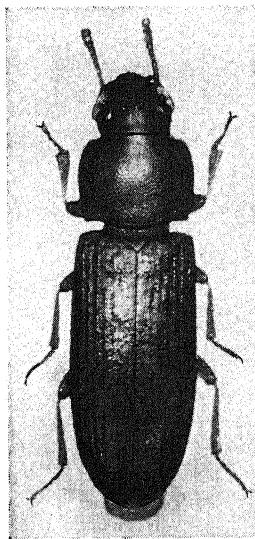
FIG. 129. Flour beetle *Tribolium confusum*, enlarged fifteen times. (*From U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine.*)

Some laboratory studies on the flour beetle Tribolium (Fig. 129) offer suggestions as to the factors involved in size of population in relation to success. In one of these studies the greatest increase was obtained by putting beetles into a culture at the rate of 1 for each 8 g. of flour. Denser and rarer populations both produced fewer offspring. The arguments offered are that in dense populations the females lay fewer eggs because they are jostled by others, and that some of the eggs are eaten by other adults and larvae, while in sparse populations there are fewer meetings between the sexes. The most successful density brings a balance between these opposing factors, one favoring dense, the other sparse, population. Temperature and humidity influenced the absolute densities that were most advantageous, but always there was a density that was more favorable to increase of population than either higher or lower densities were.

Also rated here as an advantage is the tendency of various animals to increase certain activities in the presence of others. Guppies, monkeys, chimpanzees, and men eat more in company than when alone. If the company is pleasurable, they probably digest their food better. Some goldfishes in groups of four ate more daphnias than did isolated fishes; when the grouped ones were isolated and the isolated ones grouped, the grouped ones again ate more. It was thus not just an accidental difference in the goldfishes selected for the group test. Other kinds of fishes showed similar results. None of the kinds used in these experiments show any particular tendency to swim in schools. Goldfishes and green sunfishes have been shown to learn a maze faster when

other individuals are with them than when they are alone. Cockroaches, on the contrary, learn a maze faster when alone than in the presence of others. So also do parakeets learn better alone. These birds differ in their ability to learn, and when birds of unequal learning capacity were caged together, the faster one tended to slow down. It made no difference how the caged pairs were made up as to sex, whether both of one sex or one of each, the result was the same. Children in school usually learn better in classes than by themselves under private tuition, though there may be exceptions. A species of ant (Camponotus) digs its nest faster on the whole in groups than singly. When digging alone,
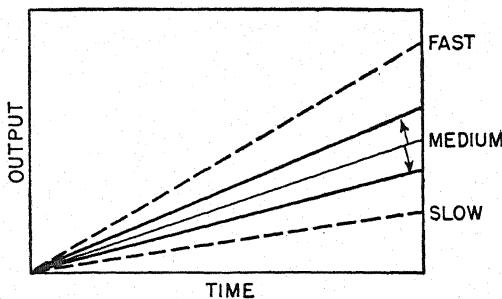
FIG. 130. Influence of fast-working and slow-working ants on medium worker. Light solid line, rate of digging of medium worker when alone. Heavy solid lines, rate of digging of medium worker when with fast worker (*above*) and slow worker. Broken lines, rate of work of fast and slow workers. (*Modified from Chen.*)

the ants differ; some are fast workers, others slow, others intermediate. When two were put together their combined output was greater, though in some combinations the faster of the two workers was retarded. For example, an intermediate ant, put with either a better or a poorer worker, tended to shift its speed toward that of its companion, either up or down (Fig. 130). Putting a third ant in a task force did not improve the output per ant any further. The most active of the ants differed in some physiological way from the more sluggish ones, for they could not stand deficient diet or drying so well.

The advantages thus far listed have not involved much organization in the group. In some other instances there is social stratification leading to cooperation, orderliness, peace, efficiency, and division of labor. These situations are specialized in such different directions as to require separate treatment.

Territoriality. The tendency of birds, lizards, mammals, and some fishes to claim and defend territories was mentioned earlier as tend-

ing to reduce the size of breeding populations (Chap. X). We need now to consider this phenomenon as it affects the economy of the group. One of the most obvious advantages of territoriality is that it spaces the population. A pair of birds can count on possession of most of the insect larvae that grow in their particular area. There is little competition between pairs, once possession of the territory is successfully established. In our capitalistic competitive human society we would probably decry the division of a field of activity among corporations by mere agreement, but among birds it apparently works well.

A second effect of territoriality is that it encourages monogamy. The permanent pairing of birds often entails help by the male in caring for the young, which is surely an advantage. It has also been argued that, since suitable territories are often not numerous enough to accommodate all the birds (or other animals), there will be a surplus of unmated females and males and that this surplus is useful as a source of replacement of individuals lost from a territory. This feature *may* work as postulated, though it is not clear just why the *certain* exclusion of surplus individuals from the breeding population is more favorable than the *possible* exclusion of some of them through breaking up of pairs. If *all* birds paired in the first place, there could easily be more breeding, even after death losses, than there would be if some were arbitrarily excluded from pairing at the beginning of the season.

Spacing the population should also help restrain the ravages of both predators and disease. Prey that has to be hunted down singly has a better chance to escape altogether, and infective germs that must be transmitted from one individual to another by contact may be effectively controlled. Escape from predators is no doubt aided by the fact that the "owner" of a territory is familiar with its hiding places and can use them promptly when concealment is necessary.

Peck Order. Within a group there is often a stratification which grades its members with respect to certain privileges. When a flock of hens is newly assembled, conflict between individuals is almost certain to occur. As between two particular individuals, one or several fights establish one of them as dominant over the other. Thereafter the winning bird may peck the loser without remonstrance. The loser of this tournament may win in relation to a third fowl, and this third fowl may win or lose in other pair conflicts. Sometimes one hen may accept an inferior position without a fight, but in one way or another a relation of dominance and subordination is established—one that is recognized and remembered by both individuals. After, say, several weeks

the society of hens is organized into a "peck order" in which one hen may peck any other hen in the flock without starting a fight. There is a second fowl which may peck any other hen except the top-ranking one. Another one occupies third rank, and so on down to the bottom hen which permits any other fowl to peck her without protest. Often there are irregularities, triangles instead of straight-line relationships (Fig. 131), but some recognized organization is regularly effected.
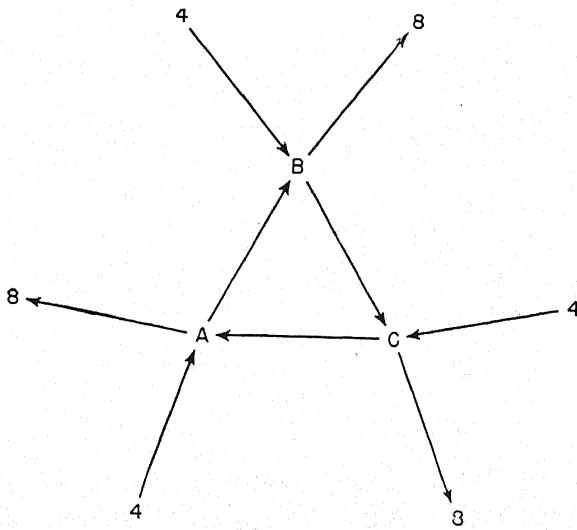
Fig. 131. Peck-order triangle in the midst of a straight-line order. Hens A, B, and C, sharing ranks 5, 6, and 7, may all peck hen No. 8 and be pecked by No. 4. Among themselves, A pecks B, B pecks C, and C pecks A. Arrow points to subordinate in any pair. (*Modified from Allee.*)

If a strange hen is introduced into a flock that has settled into a given order, conflicts start promptly. It is not usually necessary for the new hen to fight every hen in the flock to establish her place, for some low-ranking hens, doubtless observing other fights, may yield without a test. Changes in the order may occur at intervals, perhaps as a result of some physiological (hormonal) change increasing the aggressiveness of a hen of less than top rank.

Other ainmals which utilize conflicts—contacts may be a better word —to establish a social order are mammals, lizards, and fishes. The expression "peck order," adopted early for birds, does not literally express the relationship between individuals of these other vertebrate groups, and the name "social hierarchy" has been generally employed,

at least for these other groups. Man has his hierarchies; all but a few of us know people we would rather let have their way than go to the trouble of checkmating their moves.

Many things enter into the determination of dominance. In general, physical prowess wins, though experience may upset strength. Mature animals usually dominate immature ones. Size is an advantage, though an aggressive smaller animal may be the winner. Familiarity with the surroundings helps an animal on its home grounds as against a newly introduced one. Effectiveness of the male hormone is important in a social order of males. The habit of winning is helpful, at least in experiments. Thus, if a mouse of low social rank is pitted against one which it can just beat, then against a slightly higher-ranking one which it can barely master, then against a still higher-ranking one, it may be raised in rank very notably. Perhaps there is a suggestion here for educators of children in schools, relating to a gradation of the tasks assigned.

Leadership. It is probable that most animals operating in groups have their leaders. There may or may not be any connection between leadership and social rank. When a flock of hens, with dominance established in a pen, is permitted to wander over a much larger area, the leader of a foraging expedition is probably seldom the former top-ranking socialite. More often the leader is one of medium social rank. In any case, leaders, to be leaders, must be followed. Leaders are often quite as dependent on followers as the rank and file are on leaders. A hen that goes out far ahead of others on an excursion must usually stop and wait, or even return to the flock.

In mammals, the socially dominant individual seems more often to be the leader as well, though it is often difficult to identify the leader. The animal out in front is not always the leader; the leader may be in the midst of a herd or at the side or rear. There may be a number of leaders holding various ranks. In the red deer of Scotland the leader most of the time is an old female with fawn. Males make a play for leadership at the rutting season, but when danger comes they run away and an experienced female takes over.

Reindeer herds in northern Europe and Asia have what appears to be a complex organization. There is a group in the middle, consisting regularly of the same individuals, which are quiet, peaceful ones. In front of them as the herd moves is a vanguard which includes the more restless animals, the first to finish eating, first to lie down, first to chew the cud, first to rise again. Among these are the herd leaders if any can be called leaders. Certain other deer are always at the side, others al-

ways at the rear. The latter are quiet animals, not restless, not rapid runners. While organization of such a herd is clear, leadership is not marked.

African baboons live in groups, sometimes as many as a hundred animals together. When the herd moves, old males are at the edges and the rear. A sentinel or two occupy outposts when the group is at rest. How the leaders become leaders in nature is not known. In zoological gardens, the leader in movements is the socially dominant one. In rhesus monkeys also social dominance and leadership are combined. A *strongly* dominant leader takes his group over a wider range than others.

Selective Value of Group Organization. There is a strong temptation to regard whatever is as good, especially if it is prevalent. Group operations have all the marks of being useful and are generally considered to have arisen through natural selection. Much has been made of the unit of selection being the group, not the individual. Yet it is the individual that has the genes, produces germ cells, and starts the rearing of offspring. The distinction relating to the selected unit is not too important. An individual belonging to a favored society is a favored individual. If its genes are what tended to form a group or society, a society is favored as the individual is favored. Evolution is not operating on a totally new level when it produces societies or organizes them. Societies must preserve individuals of certain kinds in order to be developed through selection.

One societal organization which on its face provides the fundamental feature of selective advantage—leaving more descendants—is peck order in hens. A flock in which order of dominance has been established is a peaceful and orderly flock. Its members eat more, gain in weight, and lay more eggs than a flock kept in turmoil by introduction of strange hens. Apart from the group advantage, rank itself is associated with advantage, at least sometimes. Hens high in the social hierarchy lay more eggs, and high-ranking cocks mate more often and sire more chicks. A particularly striking coincidence of social success and reproductive success is found in the sage grouse of Wyoming, according to Scott. At the breeding season the males meet at one locality and proceed to organize themselves. When the females come later, the master cock does most of the mating. Males of lower rank copulate less frequently, and the majority of males hardly enter at all into the reproductive process.

Morphologically Distinguished Castes. In the societal organizations so far described there is no specific genetic or developmental distinc-

tion between the individuals that behave differently. While there probably are genes which tend to promote leadership or dominance in the social order, there is no sharp separation of one genetic class from another with consequent social distinction. It is quite otherwise in some of the hymenoptera (wasps, ants, bees) and termites. In the social species of these groups one of the caste distinctions is sex. In the hymenoptera the male is haploid, being developed from an unfertilized egg; the female is diploid, coming from a fertilized egg. In the termites sex is probably determined by X chromosomes. Though there must be genetic segregation of the usual kinds in these insects, the further caste distinctions do not depend on such segregation. Aside from sex, the
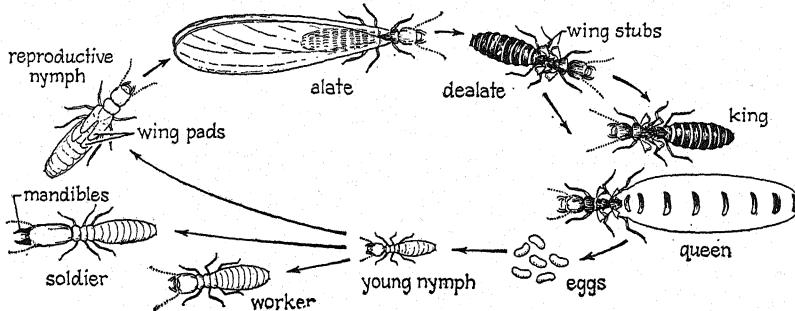
FIG. 132. Castes among termites. Note that nymphs (immature forms) may become any one of the castes. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc., after Phillips.*)

other castes of any species are produced from genetically similar eggs. A few of the particulars follow.

In primitive termites, the only sterile class is the soldier, whose job is to protect the colony; it may be either male or female. More specialized termites have two sterile classes, soldiers and workers, in addition to reproductive individuals (Fig. 132). The workers and soldiers are of either sex. Presence of mature males, females, or soldiers, respectively, prevents the production of any new individuals of the same caste in the colony. All the immature individuals (nymphs) under these conditions become workers. It is assumed that each of the other castes gives off some substance which prevents the young termites from developing into that caste; but workers are not thus inhibited. In a growing colony the queen may produce only or chiefly workers, while in a mature society colonizing reproductive individuals are produced. Many of these are present before the flight that founds new nests is started.

In the honeybee (Fig. 133), the queen and workers are genetically alike, all being females; the drones are males. Workers and drones get the same nutritive treatment; the larvae are fed royal jelly, a secretion from the glands of certain of the workers, for two or three days, then a mixture of nectar and pollen for three days. Queens-to-be are reared in larger peanut-shaped cells (Fig. 133), and are fed only on royal jelly, for 5½ days. The drones are produced in cells with slightly thicker walls. Perhaps these thick walls stimulate in the queen the closing of the duct through which spermatozoa would pass into the vagina, so that an egg laid in a thick-walled brood cell is unfertilized. The production of the several castes is evidently controlled in relation

worker　　　queen　　　drone　　　queen cell-　worker cells
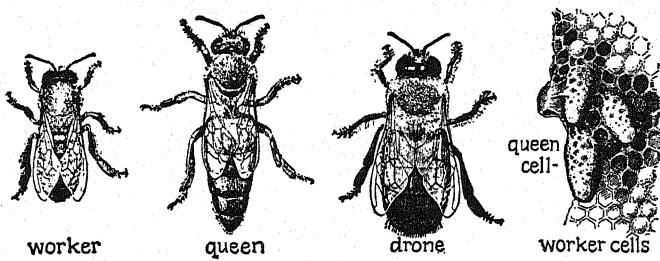
Fig. 133. Honeybee castes—worker, queen, drone—and part of comb with worker and queen cells. (*From Storer, General Zoology, McGraw-Hill Book Company, Inc., after Phillips.*)

to the state of the colony, though the precise means of supervision have eluded discovery. For some reason, a surplus of nurse workers, which will secrete an abundance of royal jelly, is produced at about the same time as larger queen cells are built. These changes are in preparation for swarming—the migration of a queen and a host of workers to found a new colony. Temperature and crowding help to determine the time of swarming, and odor from the queen serves to keep the attendant workers in a cluster.

Along with this largely environmental control of development, the honeybees have evolved some remarkable group behavior. The most extraordinary is the system of communication among workers. A worker which, on a flight from the hive, discovers a source of food returns to the hive to "tell" the other workers about it. It indicates the direction and roughly how far away the food is. Simple circling movements of the returned bee indicate a source nearby—near enough that other workers need only go out and look around. If the flowers are farther away, the informant moves about in a figure 8; when at the

crossbar in the middle of the 8, the bee wiggles its body vigorously sidewise in a dance that might be called a shimmy. If the surface on which this dance is executed is horizontal, the bee's head during this shimmy points toward the flowers. If the dance is performed on a vertical surface, the position of the body pointing to the right or left of the vertical is to be interpreted as a direction equally to the right or left of the sun. If the dancer's head is down, the flowers are in a direction away from the sun, and the positions to the right or left of straight down mean such angles to the right or left of the line away from the sun. If the flowers are only a hundred meters away, the shimmy dances at the crossbar of the 8 occur at the rate of about 4) per minute; but if the flowers are a mile away, the shimmy runs are reduced to about 16 per minute. If the sun cannot be seen, its position is judged presumably by polarized light. The plane of polarization of light coming from any point in the sky passes through that point, the sun, and the observer's eye, and the bees can probably detect the polarization.

Evolution of Animal Societies. We have seen examples of social life from the simple to the almost unbelievably complex—unbelievably in relation to the kind of animal that exhibits the complex society. These influences of individual upon individual pervade a great part of the animal kingdom. From the collections of similar individuals, living together, acting together, yet scarcely contributing anything to one another, to the structurally different castes unable to exist without the aid of other castes and paying for their help by services those others are unable to provide for themselves, runs a chain of increasing integration which could have been forged only by evolution. What the beginning stages of that evolution were, fundamentally, can only be conjectured. What its most complicated products mean, fundamentally, is baffling.

The widespread development of social organization suggests that it arose through natural selection, even in those instances which yield no obvious benefits. In the highly developed insect societies (termites, ants, bees) the advantages are so patent and the mutual dependence so complete that one is at a loss to account for them in animals as lowly as these insects. In the simplest societies, mutation and recombination of genes, with selection, may well constitute the whole evolution process; in these the individual may be essentially an automaton. It is not easy to reach that conclusion concerning the bee and termite societies. Genetically identical fertilized eggs in honeybees produce queens or workers, depending on whether royal jelly was pro-

vided for the whole 5½ days, or for only half that time. Nurse workers
are directly responsible for furnishing the crucial food; how do they
decide that one kind of brood cell is to receive royal jelly continuously,
another kind first one sort of food, then another sort? Genes could
make them react automatically at sight or at touch of the special cells.
But why are queen cells produced only at certain times? What prompts
workers to build these cells shortly before a colony is due to divide
by a swarm? Why do extra nurse workers appear about the same time?
Is there a succession of physical changes, accompanying increase of
size of population, to which the workers respond automatically? Or
do the bees somehow learn? They have been shown, in experiments,
to associate food with colored cards and to remember the association
even after it is dissolved. That is, they have a degree of intelligence.
When bees point to a discovered patch of flowers, either directly or
symbolically by imagining the sun at the top of a vertical line, are they
using intelligence, or do their genes and the food they ate as larvae
force them to adopt this behavior? It would be difficult to draw here
the correct line between biological evolution and purely social evo-
lution.

No help is derived from the concept that the animals are part of
something that is larger than they, and that it is this larger thing which
is being selected. For societies do not produce germ cells; they do not
have genes. It is often said in such connections that the whole is larger
than the sum of its parts. This is usually a mystical concept, because
the extra features besides the parts are not understood. When we
know everything about the parts, we no longer find the whole to be
greater than their sum. Emergent evolutionists used to point to water
which, they said, was not the mere sum of hydrogen and oxygen; it
was something more. Yet when the atomic structure of the elements
came to be understood, water *was* the sum of hydrogen and oxygen.
That the whole was a liquid and the parts were both gases was wholly
irrelevant. Each element contains in itself the property of making a
liquid at ordinary temperatures when joined with the other element.
We would not learn that feature unless they were joined.

So, a society *is* made up of its individuals. When we discover that
an animal does things in company that it does not do when alone, we
have merely lessened our ignorance concerning the single animal. It
had the property of behaving in a certain way in a society; we did
not discover that property until the individual was associated with
other animals. For any biological evolution of a society, we shall have
to look to its individual members. It is *their* germ cells, *their* genes,

their mutations, *their* recombinations of genes, *their* survivals, which make a society change or not and cause it to survive or perish. Society may be good; if it is, it will help its individual members, and they will preserve or promote the society.

Early Human Social Organization. There are two general ways of estimating the characteristics of early societal development among men. One is to rely on the material things or signs of activities which archaeologists discover; the other is to observe what savage tribes in
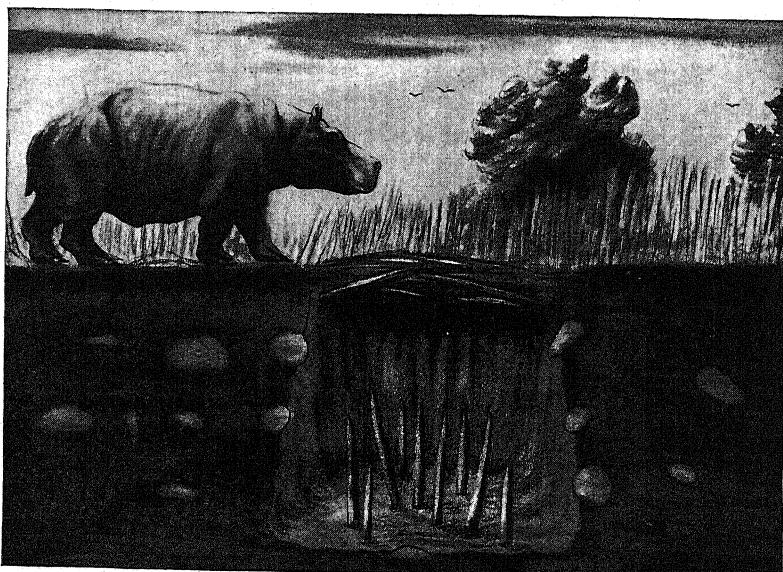
Fig. 134. Animal pitfall as it is conceived to have been used by Mousterian man. (*From Hussey, Historical Geology, McGraw-Hill Book Company, Inc.*)

various parts of the world do now. The first method provides very meager information, the second probably misinformation. Tools, pottery, piles of rubbish, bones of animals, and burial of the dead give us an idea of how men lived, but no information at all concerning working together, cooperation, rules of behavior, and the like. We draw inferences from some of the discovered objects, but they are only inferences. And as for modern savages, there is no assurance and little likelihood that their social organization has come down unchanged through ten thousand years, even if their ancestral systems had been identical with those of our ancestors.

So long as men were few and scattered there was little opportunity for group activities. There must have been family groups; the helpless-

ness of infants would seem to ensure that. Superimposed on families there were clans, especially as men increased in numbers. The clans of savage peoples now are theoretically based on kinship, but outsiders are taken in by ritual. Such clans are supposed to have descended from some animal, and that animal is the clan's totem. Hunting and fishing grounds are common property, but tools and weapons may belong to the individual. Ceremonies performed by all together produce a clan solidarity. It is a fair guess, but only a guess, that early barbarians had comparable ideas and practices.

It can be and has been argued that the hunting of large game, such as the mammoth, would have to be a group project. A single hunter could hardly have killed so large a beast. Trapping big game (Fig. 134), in which Mousterian man specialized, could not have been a one-man enterprise. It is not likely that one man or family would have been permitted to use so large a supply of food to the exclusion of others, even if he had taken it singlehanded. The logic of this argument appears adequate. Such community hunting would be cooperation and might or might not involve division of labor.

From the perfection of some tools it has been tentatively concluded that there might be specialists in the art of making them. The unity of pattern of tools in a given area would indicate that ideas of their proper construction were passed on or exchanged, whether the making was done by a few specialists or by each user for himself.

Division of Labor. While the earliest cooperation of any kind *may* have involved specialization, or division of labor, that cannot be proved. As civilization advanced, however, the nature of certain human activities is such that not everyone could have been related to them in the same way. For instance, when copper replaced stone as the material of tools and weapons, individuals were incapable of following the manufacturing operations through from beginning to end. There had to be miners, smelters, and smiths. For many social groups there had to be commerce, for copper was not available to them locally. The men engaged in these occupations were withdrawn largely or completely from the business of food production and had to be paid out of surplus food produced by those who still followed that agricultural occupation. The food producers were doubtless paid for the food with bronze tools. Shipbuilding must also have been a cooperative trade. So long as canoes were the only vehicles of water traffic, one or several men could have been the builders who at the same time kept up their production—or, earlier, their collection—of food. But ships were made of materials that had to be brought in from various places, and

the necessary techniques of construction could hardly be developed as a side line by a farmer. It is reasoned that dikes had to be built in the valley of the Nile to control its floods and that ditches must have been dug in the delta of the Tigris and Euphrates to drain the land. None of these structures has been preserved for the archaeologists of today; they merely seem necessary. A Mesopotamian town was built on a platform of reeds, which indicates the marshy nature of the ground. This rich soil, to be used for growing crops, would have to be drained. Drainage would have benefited everyone—hence one family would be foolish to dig the ditches even if that had been possible. That is the way we have to "discover" many things about social effort of early man.

The arrangement of houses in villages shows at least cooperation. In the Near East, village sites have been found to cover 1 to 6 acres, and to include 8 to 35 households. The buildings are placed in rows, along streets. This planning of village structure *could* have been merely the individuals' ideas of the fitness of things, but in relation to other people. The plan *could* represent formal agreement, or it *could* be the product of some sort of control. In any case, men were doing things in relation to other men. As villages grew to cities, the need of cooperation and organization was greatly increased. Occupations increased hand in hand with increasing variety of human wants. Men learned uses of things they found, such as metals, and got ideas of things they could make that would be useful. Communities specialized in certain products because of local supply of materials, just as earlier one community had produced superior stone implements because of local obsidian. Commerce—a separate occupation—grew up because of these specializations.

Not all regions advanced their cultures at the same rate. Civilization could grow in one area, side by side with other areas occupied by savages. It took time to spread social organization as well as industries. Even that early step, food producing, happened 3000 years earlier in Egypt than in Britain. All other advances in economic and social life were made in certain areas ahead of others. The ragged line of advance has continued into the world of today, with extremes of civilized organization and barbarian practices in different parts of the same earth.

Ruler and Ruled. From a knowledge of human nature one would expect that any group of men would soon develop a degree of authority resident in certain individuals. Be it called peck order or some more elegant name, it probably existed early. In the most demo-

cratic society today the dominance relation exits; men seem to be built that way. Yet there is no archaeological proof of its beginnings.

How chieftains came to be formally recognized as such can only be guessed. It is probable that rituals were performed, shows staged, with the idea of influencing nature, because such efforts are made in tribal societies now. Early men were superstitious and believed that incantations, displays, and art could be used to better the economic state. In a food-producing group, crops could be made better, they thought, by propitiating some being that was in control. The ritual may have been one in which a member of the group impersonated the "corn god," for example. This "corn king" received the adulation of the crowd and was the center of attention during the ritual. The impersonator may have been pleased with this temporary prestige and power, and—human nature being what it is—got ideas about maintaining his status longer. He could pretend he was a real king, not just an actor, and—again human nature being what it is—some people may have been fooled. Even in our democratic societies of today exercise of power breeds love of continued and increased power, and pretenses and deceptions are commonly used to prolong that status. And there is always an unenlightened group which can be deceived by the pretenses.

The dependence of communities on one another for needed products, which was the foundation of commerce, must early have led to wars and conquest. Just as today, some peoples are sure to have thought it easier to take what they wanted than to give something in return for it. Armies were sent along trade routes, not merely to protect those routes but in many instances to seize property. In taking material things, armies also took men, who became property. Some early illustrations picture slaves, evidently as a well-established feature of society. Thus was produced the lowest caste of human beings. Thus also was fostered increased influence of the highest classes, for military conquerors won prestige. They could boast of the slaves and other booty brought back from the wars, just as democratically elected officials now boast of the post offices, subsidized electric plants, and flood-control projects they have brought to their people. In both instances the accomplishments were at the expense of someone else. A king needs popular support, for kings can be deposed, and the military leader's conquest could easily be built up, in the mind, as favors to his people. Superstition, a natural part of human mentality, could likewise be the origin of temporal power for certain individuals. We have already mentioned the possibility that a "corn king" became a political

king, through superstition. Superstition led to the concept of gods of various sorts. Men's attitudes toward the gods constituted religion of a sort. Not many people could communicate with the gods, so someone had to "represent" them. Self-appointed conveyors of the will of the gods, perhaps claiming to have been entrusted with that will in dreams, could always get a following. Whether they ever fooled themselves into thinking they were actually possessed of supernatural insight is uncertain; strange things have happened. It seems quite pos-
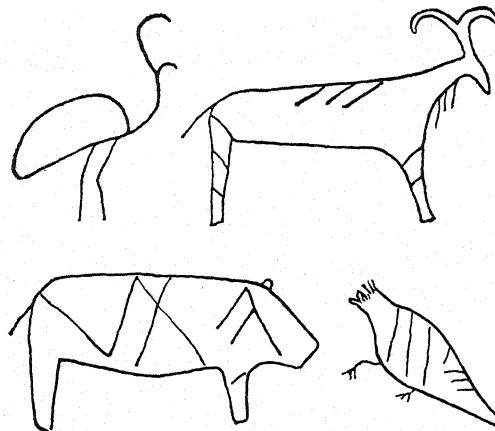
Fig. 135. Figures of animals scratched on early Egyptian pots, probably of totemic significance. (*After Childe.*)

sible that many of them were outright impostors, who loved power and knew how to get it.

In Mesopotamia the priests formed a corporation. That gave permanence to any control they exerted. Civilization had advanced to a point where division of labor was making the payments for specialized service a complicated affair, and the priestly corporation took over the process, through payments to the "gods." Actually the payments were made to the priests, who thus wielded considerable power. When political kings later developed, they did not abolish the priests. Even conquerors respected their victims' gods. Who could say what power even strange gods might have? It was safer to appease them. So, priests and kings usually worked together. It was not until about 2500 B.C. that a temporal ruler rose to a position of control over a number of states, in the Tigris-Euphrates Valley, thus forming the first empire in the Mesopotamian area. The emperor was, in that region, never quite an absolute monarch.

In Egypt there may have been less of priestly control, on the way to temporal kingship. Clans had developed extensively, with their animal totems (Fig. 135). The elephant was one clan's supposed (at least figurative) ancestor, the falcon another. Out of these clans came political organization at a higher level. Menes, the chieftain of the falcon clan, and at first the king only of Upper Egypt, became the first chief of the united state. This was about 3000 B.C. There was religion, and temples were built, but by favor of the pharaohs. Theoretically everything belonged to the pharaoh, and he had complete power. Surplus wealth accumulated by the ruler went into great tombs, whereas in Mesopotamia temples were the result of such accumulations.

At these higher levels of political organization emperors still needed prestige. They could—and did—boast of digging canals, building temples, and importing, or stealing, prized foreign goods (timber, copper). Sometimes, in pictures, the emperor was shown, dressed as a bricklayer or mason, receiving plans of a monumental public work from the gods—much as a president of a republic today, dressed in jeans and a broad-brimmed straw, might be photographed pitching hay. The king began to rule by law, which gave a semblance of uniformity to the government. A pharaoh gave instructions to tax collectors, and on paper punished those who abused their privileges, thus putting the monarch in the light of his people's advocate. That was probably as clever a way as any of maintaining power.

Conflict of Empires. It could be claimed for empires, and it was probably at first true, that they brought some sort of order out of chaos. Conflicts between the component cities or states were settled by the higher power. Peace thus reigned, much as it does in a flock of hens whose peck order has become settled. Other empires arose. But the human race was growing in numbers, territories became crowded, and robber expeditions, as they would have been called in an earlier stage, brought conflict between empires. Armies, having been wasted in wars, were recruited by mercenaries from neighboring barbarian groups. And when the barbarians had learned the more effective methods of warfare, they often turned on their employers and destroyed them. Civilization declined. Standards of living, never adequate for the lowest classes, dropped seriously. And mankind kept on multiplying.

Colonies. One solution of the population problem, in the Mediterranean basin, was the transport of groups of farmers to new areas reached by water. Outposts of empires had been established before, but they were supposed to be means of increasing the power of, or

of collecting tribute to, the rulers at home. These migrations from Greece and the Phoenician cities were designed to make more room for everybody. On the way, and after they arrived, things were happening to these emigrants. The voyage itself was a severe dislocation of the system of rule to which they were accustomed; and in the new land they were in no position to build copies of the cities or states from which they came. New systems of government were adopted— systems more like republics. Phoenicians peopled North Africa, and from there colonized western Sicily, Sardinia, and the coasts of Spain. Greeks occupied the Aegean coasts and islands, the Black Sea, eastern Sicily, southern Italy, and Marseilles, an Atlantic port. Etruscans went to west-central Italy.

Reform Elsewhere. Then liberalization began back home, at least among the Greeks. Middle classes challenged the landed overlords, gained office, expelled tyrants. Official positions were filled by lot, all attended meetings and voted themselves free drama and public buildings, to be paid for by taxing the rich. Silver mines helped pay for such things; so did tribute from neighboring states, for the Greek ideas of democracy did not extend beyond Greek borders. Athens was after all hardly a democracy, just a larger-than-usual ruling class.

Rome overthrew its Etruscan rulers, and established an oligarchy. It conferred new privileges upon the lower classes—on paper, that is— but deprived them of these advantages by administrative irregularities. Reform was something to pat yourself on the back for, not practice. One method of nullifying written reforms was to give church officials a veto on them. Rome succeeded militarily, but farmers lost their land. Rome overthrew Carthage and its dominions, then absorbed the Greek city-states, becoming a great power. But the state took control of everything, provided free baths, free shows, free food. It all ended when the barbarians from the north descended upon Rome.

Struggle for Democracy. We can no longer dwell on details. After a long intellectual eclipse, the general trend of human social organization became one of rise in the power of common men to guide their own affairs. Sometimes in this process lords were merely extracting concessions from their kings, leaving the people in pretty much their old dire situation. Sometimes the people wrested privileges from their immediate rulers. Colonization had the same effect as in the migrations from Mediterranean states; it permitted the spreading groups to throw off the system that had governed them and to erect new governmental procedures on new democratic principles. Democracy in the

colonies then reacted on the mother countries, helping the democratizing process in them.

In recent years it has proved possible for small groups of selfish and determined men, using prejudices, pitting class against class, to obtain political control over a large part of the Old World. Cruelties not exceeded even in barbaric societies have enabled them to destroy, in several decades, all the democracy that had developed in their particular areas in several centuries.

It is not our task to predict. We are examining the course of social evolution in man with a view to relating it to evolution of other things if any such relation exists. It may be said, however, that man has come out of a number of cataclysms of a social sort, at various places on the earth, and at the present enjoys, on parts of his globe, a freer social organization than existed in any previous century. There are occasional signs that he may yield his acquisitions by default, but that is probably in his own hand to determine.

Nature of Human Social Evolution. How long did men require for their major social evolution? The Old Stone Age was roughly the Pleistocene. The last of the great glaciers retreated at a time variously estimated at 15 to 25 thousand years ago. The New Stone Age, in the faster developing civilizations, lasted hardly two thousand years. Piecing times together we may estimate that the societal evolution described above for man almost all occurred in the last ten thousand years. Most of it took place in the last six thousand years.

The unit of time in biological evolution is the generation. Between generations is the only time at which genes may recombine or new mutations enter into genetic constitutions. In the period occupied by human social evolution man may have passed through an average of 250 to 400 generations. For the same number of generations Drosophila would require ten to twenty years in a semitropical setting. In that time no one could suppose that Drosophila would undergo any important evolution. Similarly, there could have been little biological evolution in mankind in the last hundred centuries. We are genetically not very different from our ancestors of early postglacial time.

This does not mean that we are not different, genetically, from other men of today. It is obvious that there are such differences. But the common stock from which mankind came goes back fifty or a hundred times as far as does the beginning of social evolution.

Social change, it is clear, has not depended on genetic change. Man has used his intelligence to gain mastery over natural things and phenomena. First he made tools. Then, learning the art of toolmaking

from his elders, he made better tools. Every step depended on what went before; social development was a real evolution. Man could not have jumped into the Bronze Age directly from his pretool state.

Superstition also entered into social evolution. It led to rituals, and rituals probably led to religious and political domination by leaders. How superstition is related to genes is not clear. All races of men have exhibited it in some of their members, perhaps in all of them. No one is a good judge of his own superstition; it is not something easily detected by introspection. So, while intelligence is clearly a genetic product, superstition is not clearly so.

There may be an important contrast between intelligence and superstition in relation to social evolution. Intelligence seems best fitted to have led to man's higher attainments in science, literature, and perhaps art, while superstition guided him into his religions, social stratification, and systems of government. His changes in all of these would have been evolution, but none of them biological evolution—none of them the result of mutations or recombinations of genes occurring in the few thousand years that saw this social change.

It is important to point out that social evolution is not necessarily independent of genes. It is highly probable that civilization in general has been different in different regions partly because of the genetic constitution of the people. Tendencies toward science, or engineering, or invention, or art, or philosophy, or mysticism are almost certainly not due just to environment. When one says that a people lacks mechanical genius—such statements may or may not be true—it does not mean that some of them, transplanted into an industrial community, could not learn to run or to make machines. It means only that, left to themselves, they would not have developed a civilization in which machines were a very important element. Statements that certain peoples do not have certain capacities are usually based on prejudice and may be very mistaken. Yet it must be true that races do differ in such respects.

Confusion of the one kind of evolution with the other is common. To the average man evolution is evolution. In particular, the evolution of man is not seen to be of two radically different kinds. Clear thinking is needed on this distinction, in relation to the past, and in any attempt to guide or even forecast the future.

CHAPTER XV

ORIGIN OF LIFE

> The carbon of the sun's atmosphere does not represent or-
> ganic matter, but the exceptional capacity of this element to
> form long atomic chains and to unite with other elements, such
> as hydrogen, oxygen and nitrogen, is the hidden spring which
> under proper conditions of existence has furnished the impetus
> for the formation of organic compounds. Similarly, protein is
> by no means living matter, but hidden in its chemical structure
> is the capacity for further organic evolution which, under cer-
> tain conditions, may lead to the origin of living things.
> —A. I. OPARIN, 1936

We have left to the end of the story of organic evolution the very
first of its general phases. Life has not always existed; it is clear that
conditions of the earth in its own early stages could not possibly have
furnished the materials involved in life processes or have permitted
the interchange and sequence of events that characterize them.
Enough is known or reasonably concluded concerning the origin of
the earth, the nature of the solar system, and the aging of the stars on
the one hand, and of the chemistry of proteins, the physical features of
colloids, and mediation by enzymes on the other, to render it certain
that substances and phenomena of the latter class could not coexist
with those of the former. There was no life on the earth when that
planet was molten, nor when it was a cosmic cloud, nor for a long
time thereafter. No satisfaction accrues to a biologist—hardly even to
a philosopher—from redefining life to make it fit both early and late
stages of what was happening on the earth. Calling internal motion
life, so as to bring hot gases and molten rocks or swirling dust storms
within the pale, is a mere verbal exercise; it contributes nothing to the
understanding of anything; it does not even unify thought. Life accord-
ingly did not go back to the beginning of time; it must have come into
existence within the period of the earth's own evolution.

Genesis of Theories of Life's Origin. One who would discover the
origin of something naturally looks at the end product first. That has

been the procedure in tracing all lines of descent. Speculation concern-
ing the evolution of organs of vision started from knowledge of the
modern vertebrate eye. The author of the fin-fold theory looked at the
appendages of vertebrates first. The great genealogist who started evo-
lution with the moneran realized from the beginning that at the other
end of the chain stood man.

Those who concerned themselves with the origin of life, if they ad-
vanced a theory, were obligated to assure themselves that the workings
of the theory would lead to present-day protoplasm. What are the char-
acteristics of this living substance? For one thing, it is largely made of
proteins. While there are other types of organic matter in animals and
plants, their share in the life processes is minor. Carbohydrates and
fats are storehouses of energy, but proteins determine what organisms
are like. It is the proteins that make one animal persistently different
from another. It is the proteins that characterize living things. Second,
protoplasm is colloidal. This means that it consists of sizable particles
dispersed through some continuous medium—a liquid in the case of
protoplasm. While the colloidal particles in protoplasm may be single
molecules, they are much larger than the molecules of a sugar or the
ions of a salt in solution. This large size of the particles entails certain
properties related to permeability; and particles, whether small or
large, confer on a colloid certain physical qualities because of their
enormous aggregate surface. Then, finally, protoplasm contains en-
zymes, which are to biology what inorganic catalysts are to industrial
chemistry. They hasten reactions between other substances without
seeming to participate in those reactions. Living things contain hun-
dreds of enzymes, doing hundreds of different things. These agents are
protein, but are so specific in their actions as to be considered a class
by themselves.

There are other characteristics of protoplasm which it may be nec-
essary to mention in certain connections, but the three named will il-
lustrate the building of theories of the origin of life.

Differing Emphasis in Theories. Early theories of life's beginning
seized upon one or another of the major features of protoplasm and
sought to explain it. Other features were passed over lightly. Origin of
the proteins was the approach of some of the theories. Proteins are
composed essentially of carbon, nitrogen, hydrogen, and oxygen. One
of the theories recalled that carbon and nitrogen combine into the
cyanogen radical (CN), that nitrogen and hydrogen, and hydrogen
and oxygen similarly combine—all at high temperatures which the hot
earth presumably furnished. Another approach to the proteins was

through the formation of nitrogen oxides and ammonia (NH_3) by the action of lightning in the atmosphere. This would have occurred when the earth was relatively cool. These substances, washed into the soil where carbon dioxide was supposed to be waiting in abundance, and there acted upon by solar energy, were believed to form proteins.

Colloidal structure furnished the starting point of one or more theories. How colloids happened to be formed was a mystery, being attributed, in the chief theory of this type, to a law of complexity which was itself a mystery. More complex substances were held to be produced whenever conditions became right for their production, and the conditions themselves were partly a consequence of this trend to complexity.

A third type of theory emphasized the enzymes. How these catalytic agents arose was hardly explained; the theory dealt mostly with how enzymes got into protoplasm. The general method was held to be that the enzymes produced the protoplasm around themselves. Bringing about chemical reactions, the enzymes were in the midst of the substances which those reactions produced. Protoplasm thus incorporated the things which made it; the architect and mason were being built into their temple.

Passing over these early theories so hurriedly calls for no apology. There are sound reasons for concluding that none of them could have been correct. While any other theory proposed in their place may also be incorrect, at least in detail, it seems fairly certain that the ones so far described are untenable. Oparin in his "The Origin of Life" has presented a carefully reasoned argument concerning what would have been possible and what might have been probable—even almost certain —which leaves no room for acceptance of the old theories. His account is in general followed in the remainder of this chapter, but with occasional diversions for which he is not responsible.

Faults of Older Theories. All the early concepts of the origin of life were based on the assumption that that origin took place in a relatively short period of time. How short a time was supposed to be involved is not directly stated by any of the authors; but by implication the beginning of life in each of the theories was regarded as depending on a fortunate combination of circumstances that might easily never have happened. According to them, this might have been a lifeless world but for a happy concatenation of more or less random events. A theory should not be rejected *merely* because it rests on accident; man should not throw away a concept just because it engenders in himself an uncomfortable feeling that he narrowly missed being omitted from

the picture. When, however, careful consideration of the history of the earth indicates that opportunities for producing living matter were presented over and over again, and not just here and there but all over a large part of the planet, views that portray the origin of life as a happy accident look at once improbable. Life might rather seem inevitable; it is more likely that life could not have avoided being produced.

Another weakness of the old theories is that some of the materials which their authors thought they could draw upon to produce living matter probably did not then exist on earth. These authors all thought carbon dioxide was the primary carbon compound, that it was available in abundance, and that from it the first organisms got their carbon. Now it appears that this substance was the end of the carbon cycle of evolution, not its beginning, and that most of the carbon dioxide later in existence was produced by organisms. Carbon monoxide was postulated as part of the atmosphere of the hot earth, on the basis of certain bands in the spectrum of stars, but these bands have been shown to be due to the dicarbon molecule C_2. The atmosphere *did* contain the water vapor that was generally supposed to be there. The precise composition to be assigned to the earth's atmosphere, as bearing on the origin of life, depends on what stage of this planet's existence witnessed that origin. Theories differed concerning that time. Accordingly it seems best to close this statement of the patent weakness of the old theories and turn to some of the facts on which presumably better concepts must rest.

Atmosphere of Stars. Stars differ in their brightness, depending on their temperatures. Their colors range from white, with a surface temperature as high as 28,000°C., through yellow, to red and dull red with surface temperatures as low as 1800°C. Our sun is yellow, and its surface temperature is 6000 to 8000°C., except in the sunspots, which are around 3000° cooler. We are interested in these temperatures largely in relation to what they do to carbon. This element is the principal component of living matter. It is so partly because its valence is four; that is, it can combine with four elements or radicals whose valence is one. Carbon forms the major part of the skeleton of organic molecules, and it is likely to have been intimately concerned in the formation of the first living things. Now, in the hottest stars, carbon is mostly ionized; it is not even in the form of atoms. Any carbon compounds would be out of the question. At temperatures below 20,000° carbon appears as the element—that is, it is not ionized. At perhaps 10,000° the first compounds of carbon occur; they are unions with nitrogen (the cyanogen radical CN) and hydrogen (the hydrocarbons). These are the only

forms in which carbon combines with anything in the atmosphere of
the stars: with itself (C_2), with nitrogen, and with hydrogen—*not* with
oxygen.

Our sun's atmosphere contains carbon in these three combinations.
The position of carbon in the sun's atmosphere is of interest. From the
low atomic weight of carbon, only 12, one would expect it to float well
up among the sun's gases, but actually it is down to within 500 miles
of the sun's visible surface (Fig. 136). Partly this is due to the fact that
carbon requires 3000° to liquefy and much higher temperatures to be-
come gaseous. Partly, also, its low position is caused by its tendency to
aggregate into heavy collections of molecules. The dicarbon C_2, whose
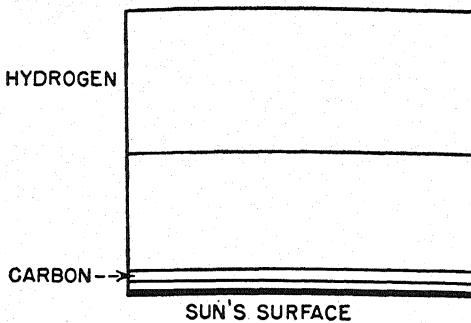
FIG. 136. Sector of sun's atmosphere showing position of carbon and hydrogen.

spectral bands were once thought to indicate carbon monoxide, is but
a mild consequence of this tendency.

Origin of the Earth. According to one theory, about three billion
years ago another star at least as large as the sun approached the latter.
If only as large as the sun, it would have had to come within a million
miles to have done what is attributed to it. At that short distance the
force of gravity between the stars raised a great tidal wave on the
gaseous and liquid sun and drew off into space a long elliptical mass
of its material. This material condensed at various points in the ellipse.
The larger condensations near the middle formed the planets Jupiter
and Saturn. At the end of the ellipse away from the sun smaller con-
centrations produced Uranus and Neptune, while nearer the sun were
the still smaller Mars, Venus, and the earth. According to this theory,
the earth started with a hot atmosphere essentially the same as that of
the sun.

Another theory holds that the earth began as a cold cosmic cloud,
which must have been separated from a larger cloud which became the

planetary system. The particles in this cloud would have been solids and gases. Friction of the particles as they "fell" toward the center of the cloud would have generated heat. Furthermore, radioactivity of certain isotopes included in this cloud may well subsequently have released sufficient energy to raise the temperature of the mass by a few thousand degrees.

Whether the early earth was a hot gaseous mass that condensed on cooling or a huge cloud of cold particles that merely settled by gravity, heavy things would have gone to the center. The heavy metals, largely iron, came to form a central core some 4000 miles in diameter, which either was from the first or probably later became molten. During this centripetal movement of the heavy metals, carbon must have been caught and carried down. At any rate meteorites, whose composition must be similar to that of the core of the earth, contain carbon compounds. As the earth's core later cooled to the point where

$$3 \, Mg + N_2 = Mg_3N_2$$

$$2 \, Al + N_2 = Al_2N_2$$
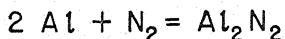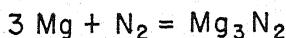
Fig. 137. Formation of nitrides.

chemical union could occur, carbides would be produced, since these are the most stable of the carbon compounds at high temperatures. The carbides are the form in which carbon occurs in meteorites.

Hydrocarbons. The atmosphere of the earth could have contained no oxygen. Nor could it have contained the element nitrogen. Some nitrogen is present in compounds in the earth's present crust, but the elements nitrogen and oxygen now in the atmosphere were introduced much later, presumably through the action of living things. Water vapor, superheated, was present in the early stages. This early atmosphere was separated from the carbides of the core by the early-formed crust of the earth, but it must be supposed that the crust cracked frequently, allowing the core material, with its carbides, to flow out over the surface.

The meeting of carbides and superheated steam must have produced the simple hydrocarbons, compounds of carbon and hydrogen. These would have been produced whether the earth was first a hot gaseous mass or a cold cosmic cloud subsequently heated by friction and radioactivity. Petroleum consists of hydrocarbons. The hydrocarbons are now regarded as organic substances, since they are regularly produced in association with living things. It is entirely proper to apply the same class name to these substances formed when there were no living things. The hydrocarbons were thus the primary organic compounds. It is important to note that the first carbon compounds on the earth's

surface were not the oxides but the reduced forms, hydrocarbons. Their production was one milestone on the way to life.

Nitrides and Ammonia. Nitrogen had a similar history. Its oxides, at high temperatures, easily dissociate into nitrogen and oxygen; hence they could not have persisted. Nitrides of iron or calcium or aluminum or magnesium would be more stable and would be rapidly formed (Fig. 137). Nitrides with water vapor would produce ammonia (NH_3); or carbides and nitrogen would first form cyanamides, and these with superheated water vapor would give ammonia as one of the products (Fig. 138). The ammonia would become part of the atmosphere of the earth, as it is of the atmosphere of some other planets. And so,

$$CaC_2 + N_2 = CaCN_2 + C$$

$$CaCN_2 + 3H_2O = CaCO_3 + 2NH_3$$
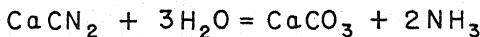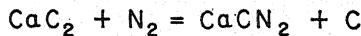
Fig. 138. One way of producing ammonia—through cyanamides.

nitrogen, like carbon, early appeared on the earth's surface not as oxides but in its reduced state, ammonia (NH_3).

The great variability of these reduction products, especially the hydrocarbons, makes it difficult to choose the most probable of their transformations as leading to life. Yet this capacity to enter into endless changes makes it all the more certain that life had its beginning in some of their derivatives. Certainly nothing that could be called alive has yet arisen; but it is a mistake to conclude that evolution of life has not begun. The groundwork—the *necessary* groundwork—for the development of protoplasm has been going on (accepting for the moment the gaseous origin of the earth) in the atmosphere of the stars. The production of carbides and hydrocarbons, of nitrides and ammonia, was part of that evolution.

Transformations of Hydrocarbons and Ammonia. The presence of water vapor permitted the H_2O molecule, split into H and OH, to enter into combinations with the hydrocarbons and ammonia. Alcohols, aldehydes, ketones, and organic acids must have come in profusion from the hydrocarbons. With ammonia, these substances would give rise to ammonium salts, amines, and amides. By the time the earth had cooled enough for water vapor to condense and fall as rain and produce hot oceans on the earth, this water must have contained many of the mentioned substances in solution. The raw materials of these types can be made into a great variety of organic substances in the laboratory today, and there is every reason to assume that comparable substances were

formed in that early ocean. As in the laboratory, so in the natural situation, the three fundamental forms of chemical transformation must have occurred. First, carbon atoms must have joined in longer and longer chains, a process called *condensation*. Second, two organic molecules must often have joined through the mediation of an atom of oxygen or nitrogen, a union called *polymerization* (Fig. 139). Third, *oxidation*, largely through the hydroxyl ion (OH) of water, must have occurred. Each of these kinds of reaction has its opposite: carbon chains are divided; complex molecules are hydrolyzed; oxidized products are reduced. All these processes go on in living things now; they can be performed in laboratories; they must have occurred in the ocean,
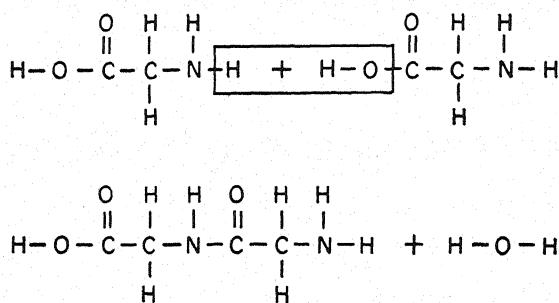
FIG. 139. Polymerization of amino acid.

though much more slowly, before there was any life. Simple sugars and the organic acids must have been among their products.

Higher Organic Compounds. Among the organic acids are the amino acids, of which proteins are composed. The amino acids may have come from other organic acids interacting with ammonia. Amino acids may be combined (Fig. 139) with one another through the nitrogen atom of their NH_2 radicals and the carbon of their COOH radicals, forming polypeptides. These substances are well along on the way to being proteins, which are the characteristic class of organic substances in protoplasm. None of these would be regarded as alive, but life was evolving.

While proteins are of special interest in connection with the first protoplasm, other organic substances were produced in the early ocean. Among these were the lipids (fats and fatlike substances), some of which are today important components of cell membranes. Substances akin to the cellulose of plant-cell walls, to silk, and to the keratin of hair must have been produced. All of them must have experienced the

three fundamental types of chemical reaction listed above; many of them must have developed molecules of high molecular weight. The water of the ocean should have contained a complex mixture of such substances.

Colloidal Structure. In the laboratory, substances with such huge molecules form colloidal solutions in water. By adsorption of water on their radicals, closely next to the particle, loosely at a distance from it (Fig. 140), the colloidal particles are kept from clumping. However, by electrical and other changes the outer, loosely adsorbed water may be removed, and the particles may clump (Fig. 141) into localized gels. The colloidal mixture thus comes to consist of gels of various sizes, separated by the continuous liquid substance more or less free of particles. The gels are still fluid but are rich in the colloidal substances. How firmly the particles are held together in such a group depends on their electric charges and temperature. A collection of particles of different colloidal substances has properties that

Fig. 140. Part of colloidal particle, with molecules of water tightly adsorbed near it, loosely adsorbed at a distance. (*After Oparin.*)

differentiate it from one made up of a single kind of particle. In any case, the gel adsorbs other substances held in the surrounding liquid, thus forming a sort of membrane around itself.

These are laboratory processes, but it would seem inevitable that, in the hot oceans of the young earth, the primary proteins (polypeptides), lipids, and carbohydrates of high molecular weight would be produced. Mixtures of these things must have produced the separate collections or gels just described. The separation of bodies of organic substances from their liquid medium confers on these bodies one of the properties of living things; they are in a position to interact in various ways with that medium, their environment. The adsorption of substances in the environment, with the incorporation of some of those substances into the gels, is not very different from growth. The parts added could hardly have been uniformly distributed, and an elementary structural organization would have resulted. The stage is almost set for the first organisms.

Natural Selection. Not all the structurally differentiated groups of colloidal particles would persist. Any which developed a particularly efficient method of growth would have an advantage. If the reactions which incorporated new materials went faster in certain gels, these

would increase. Any substance whose surface conformation served to hold two different molecules in close association would enlarge the gel in which it occurred. Enzymes would thus be favored by selection.

Size would soon prove an obstacle to the rapid reactions which induced the growth. Separation of a rapidly growing gel into two parts would permit a continuance of rapid growth, though the advantage of division would not be the cause of division. Moreover, division that destroyed the system which ensured rapid growth would be a great disadvantage. If any type of gel that had the capacity for rapid growth should, among its processes, develop also the adsorption of like by like
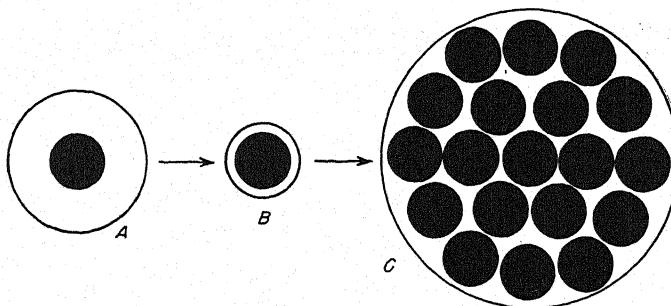
Fɪɢ. 141. Aggregation of colloid particles into a gel. *A*, separate particle with both tightly and loosely adsorbed water, indicated by outer circle; *B*, particle minus its loosely held water; *C*, aggregation or gel. (*Modified from Oparin.*)

after the manner of duplication of genes postulated in Chap. VIII, the first advantage would be preserved and a new one gained. A system that worked well would continue to grow, but would not become obstructively large, and would maintain the characters which made it successful. Reproduction in modern organisms accomplishes just these things, and it is possible that something comparable to the formation of gene copies was the earliest form of reproduction.

When Life Began. At several points in this account it has been stated that the products then formed were not alive, but that they were steps in the evolution of life. An inquiring mind that wants definitive answers to its questions may ask just where in the supposed chain of events life did originate. To answer would be as difficult as to stand up in a row a hundred men ranging from 5 to 6½ feet in stature, and say precisely where tallness begins. Any answer to the question would depend on a definition, and definitions are frequently futile. When a definition requires drawing a line across a graduated process, it may even confuse rather than clarify. If a process is understood, and if names *must*

be applied to parts of it, the exact delimitation of these parts is often not too important.

Probably anyone would say that life existed when some substance could accurately duplicate itself. That substance would already have acquired the power of growth, so that growth and reproduction could be the criteria of life. But what if reproduction were at first *not* an *exact* duplication? It was probably not a precise process at first, and the dividing line across this graduated phenomenon presents all the difficulties that pertain to arbitrary distinctions in general.

When Evolution of Life Began. No better success attends an endeavor to say when life evolved or when it began to evolve. If reproduction were taken as the criterion of life, it would be foolish to limit the origin of life to the actual processes of duplication. How the duplication came about depended intimately on the nature of the thing duplicating; *its* origin should be included in the evolution of reproduction. If growth be regarded as the first phenomenon of life, the time at which life originated is set back to a much earlier period. And that period would be just as hard to define as anything else that arose gradually. The groundwork for growth was laid long before any actual increase occurred, and forming that groundwork was part of the evolution.

Producing the simple organic substances was part of the evolution we seek to understand. The elements of which these compounds are composed also had to come into existence. Life has thus not evolved in one short period, even if "short" be made to apply to a few million years. For the beginning of the evolution of life we shall have to go back at least to the cooling of the stars or to the cosmic cloud.

Could Life Originate Now? All along the course of evolution, what happened depended on what was already there. Nothing was produced until the basis for its production was established. Hydrocarbons could not be produced until there were carbides. Ammonia similarly awaited nitrides. Amino acids awaited both hydrocarbons and ammonia. Proteins could not be formed until there were amino acids. In general, there had to be organic substances before there were organisms. The evolving organisms "fed" on the evolved organic materials.

In a more literal sense, present-day organisms feed on organic substances. A large majority of the species of living things require that organic materials be elaborated for them. All but a few kinds of animals are for this reason ultimately dependent on plants for their sustenance—the exceptions being those animals which are on the border line of plants. The bacteria and fungi also require organic matter. The

organic matter which animals, for example, consume need not be alive. Indeed, it is not alive when incorporated in animal protoplasm, even if it was alive when devoured; the digestive and assimilative processes would destroy whatever peculiar features made the matter living. Any organic matter that existed, whether produced by organisms or not, would be suitable for animal nutrition if only it were the right kind of matter.

Under these circumstances, what chance would living substance have of originating independently of living things now? Probably none. We may pass by the early stages of the evolution of life, since the late ones illustrate the obstacles just as well. Proteins, when first formed through

$$C_6H_{12}O_6 = 2CH_3CH_2OH + 2CO_2 + 28 \text{ CALORIES}$$

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O + 674 \text{ CALORIES}$$
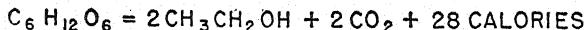
FIG. 142. The energy released by a simple sugar through oxidation (*below*) as compared with fermentation. The alcohol CH_3CH_2OH in the upper equation still retains much energy.

the polymerization of amino acids, were not alive. Suppose that proteins arose in that manner now, outside of organisms. They would be in bodies of water, all of which were peopled by animals of many present-day species. They would merely be part of the supply of organic matter on which the modern animals would draw for food. If there were an excess of this organic matter, the animals would flourish, and soon there would be no excess. The chance that any organic substances arising *de novo* would escape being utilized as animal food, and continue to escape over the long period that would be required to evolve the essential features of life, may be rated as zero. It is practically inconceivable that life could arise anew where so much life already exists. The time for life to originate was when there was no life.

The interdiction of new life through exhaustion of its food might have stopped the first life at an earlier stage. This possibility stemmed from the early source of energy. At present the source of energy of organisms is chiefly oxidation, though there are living things that get along without free oxygen. In the early stages of the evolution of life, however, there was practically no free oxygen. Energy was obtained—much less abundantly—from fermentation. The reason for the low energy release is that fermentation results in alcohol, acids, or other substances which still retain much potential energy. This fermentation was using up much of the organic matter in the primitive ocean, and replacing it with alcohol, carbon dioxide, lactic and butyric acid, and

so on. That depletion *could* have gone on to exhaustion. What prevented that from happening was the development, in some organisms, of a pigment which enabled them to use the energy of sunlight. Chlorophyll is that pigment in green plants, but there are others. The photosynthesis which these pigments permit yields oxygen as a by-product. As this gas accumulated, organisms could begin to use oxidative processes as a source of energy, and oxidation released many times as much energy as fermentation had provided (Fig. 142). Oxidation yielded carbon dioxide as a by-product, not only in life processes but in the decay of dead bodies of organisms. The raw material of continued photosynthesis was thus assured.

Once the organisms that could use the radiant energy of the sun became established, there was no longer any danger of the exhaustion of the supply of organic substances needed by the organisms that could not get their energy directly from the sun. Photosynthesis may have saved the day for the kind of life that existed before that process arose—that is, for life that depended on organic substances already elaborated. Man belongs to the latter class of organisms and is completely dependent on photosynthesis in plants.

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